

# THE WINGS OF INSECTS.

---

A SERIES OF ARTICLES ON THE STRUCTURE AND DEVELOPMENT  
OF THE WINGS OF INSECTS, WITH SPECIAL REFERENCE  
TO THE TAXONOMIC VALUE OF THE CHARACTERS  
PRESENTED BY THE WINGS.

BY

JOHN HENRY COMSTOCK,  
Professor of Entomology in Cornell University,

AND

JAMES G. NEEDHAM,  
Professor of Biology in Lake Forest College.

---

[Reprinted from *The American Naturalist*, with the addition of a Table of Contents.  
124 pp. 90 Figs.]

---

ITHACA, N. Y.  
THE COMSTOCK PUBLISHING CO.  
PRICE \$1.00.



#### CORRECTION.

The use of the expression "cuticular thickenings" on page 45 is unfortunate. For a discussion of the nature of the pale bands designated by this term, see the last article of this series, page 858.





## CONTENTS.

---

CHAPTER.	VOL. XXXII. PAGE
I.—AN INTRODUCTION TO THE STUDY OF THE HOMOLOGIES OF THE WING-VEINS, .....	43
II.—THE VENATION OF A TYPICAL INSECT WING, .....	81
III.—THE SPECILIZATION OF WINGS BY REDUCTION.	
I. Introduction, .....	231
II. The Venation of the Wings of Certain Plecoptera, .....	237
III. The Venation of the Wings of Psocus, .....	240
IV. The Venation of the Wings of Cicada, .....	243
V. The Venation of the Wings of Heteroptera, .....	249
VI. The Venation of the Wings of Lepidoptera, .....	253
VII. The Venation of the Wings of Trichoptera, .....	256
VIII. The Venation of the Wings of Diptera, .....	335
IX. The Venation of the Wings of Hymenoptera, .....	413
X. The Tracheation of the Wings of Hymenoptera, .....	420
XI. The Venation of the Wings of Embiidæ, .....	423
XII. The Venation of the Wings of Coleoptera, .....	561
IV.—THE SPECIALIZATION OF WINGS BY ADDITION.	
I. The Development of Accessory Veins, .....	769
II. The Suppression of the Dichotomous Branching of Veins, .....	774
III. The Venation of the Wings of Odonata, .....	903
	VOL. XXXIII. PAGE
IV. The Venation of the Wings of Ephemerida, .....	118
V. The Tracheation of the Wings of Orthoptera, .....	573
V.—THE DEVELOPMENT OF WINGS.	
I. First Appearance, Position, and Growth of Wings, .....	845
II. Origin of the Tracheation of the Wing, .....	851
III. The Behavior of the Hypodermis, .....	853
IV. The Tracheæ and the Hypodermis, .....	858



# THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

## CHAPTER I.

### *An Introduction to the Study of the Homologies of the Wing-Veins.*

It is the purpose of this series of papers to present a summary of what is known regarding the structure and development of the wings of insects, to give the results of some investigations in these fields made by the writers, and to indicate the value in taxonomic work of the characters presented by the wings.

As the growth of our knowledge naturally proceeds from a study of the obvious facts of nature to those that are more deeply hidden, it seems best to discuss first the structure of the wings of adult insects and to postpone for a time the study of the beginnings of wings. It will be necessary, however, to take up early in the discussion a study of the structure of the wings in those stages that immediately precede the adult stage, the pupæ of insects with a complete metamorphosis, and the nymphs of insects with an incomplete metamorphosis. It is in this field that we have the most to offer that is new.

Several writers have appreciated the fact that much light can be thrown on the problem of determining the homologies of the wing-veins by a study of the tracheæ that precede them in the wings of immature insects. The more important of the contributions that have been made to this phase of the question are those of Brauer and Redtenbacher<sup>1</sup> and of Spuler.<sup>2</sup> Still, comparatively little has been done in this direction.

This is doubtless due to the difficulties that have stood in the way of work of this kind. The tracheæ of the wings of pupæ and nymphs are often very delicate, and when filled with

<sup>1</sup> Brauer und Redtenbacher, Ein Beitrag zur Entwicklung des Flügelgeäders der Insecten. *Zool. Anz.*, 1888, pp. 443-447.

<sup>2</sup> A. Spuler, Zur Phylogenie und Ontogenie des Flügelgeäders der Schmetterlinge. *Zeit. f. wiss. Zool.*, Bd. liii, 1892, pp. 597-646.

the medium in which a wing is mounted for microscopic study they are usually invisible. It is not strange, therefore, that they have been studied so little. But in the course of our investigations we have devised a method of study of the wings of immature insects which renders the observation of the tracheæ in them a simple matter.

If a living pupa or nymph be placed in formol (4%) the tissues of the wings will be rendered translucent in a short time. In the case of very delicate insects only a few hours

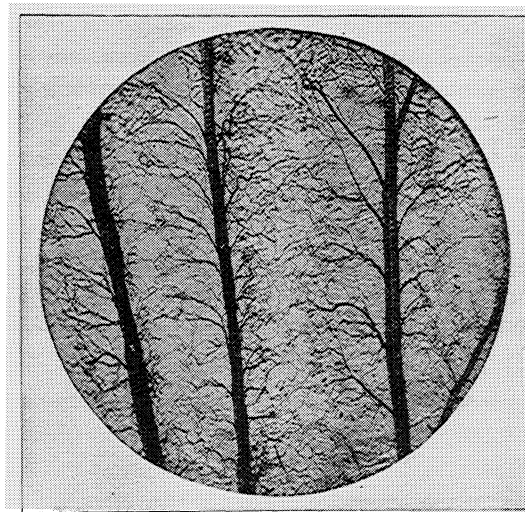


FIG. 1. — Part of a wing of a pupa of *Corydalis cornuta*.

are required for this, but with larger ones with more opaque wings it is necessary to leave them in the formol for several days, or even for several weeks. While the formol renders the tissues translucent, it does not soon penetrate the tracheæ, which are, therefore, left filled with air, and appear as dark lines when the wing is examined with transmitted light. Just after molting some wings are translucent, but there are few so clear that a short stay in formol will not make them clearer.

In order to study wings prepared in this way, they are removed from the body and mounted in glycerine jelly, care being taken to cool the mount quickly so that the jelly will not

penetrate the tracheæ. In this way most beautiful objects can be prepared, which will show the minutest ramifications of the tracheæ.<sup>1</sup> Fig. 1 is a half-tone reproduction of a photograph of an object prepared in this way. This figure represents a small portion of a wing of a pupa of *Corydalis cornuta*.

Not only can the tracheæ that precede the wing-veins be studied in this manner, but, if the wing be taken at the right stage, the cuticular thickenings destined to form the wing-veins, as well as their corresponding tracheæ, if there be any, can be seen. Figs. 2 and 3 are half-tone reproductions of photographs of wings taken at this stage.

There is, however, one undesirable feature of preparations made in this manner; it is that after a time the cuticular thickenings become indistinct, and the glycerine jelly will penetrate the tracheæ, rendering all except the larger ones invisible. But as it is a very easy matter to photograph such preparations, and as a series of photo-micrographs are much more easily compared than a series of microscopic slides, this feature does not materially impede an investigation of this kind. Usually the cuticular thickenings show best as soon as a mount is made, while the tracheæ stand out more sharply twenty-four hours after mounting, because of the clearing effect of the glycerine jelly upon the cuticular parts. It is, therefore, frequently desirable to make, at different times, two or more photographs of the same specimen.

<sup>1</sup> In making mounts of this kind our usual procedure was to spread a drop of melted glycerine jelly on a slide and allow it to cool; then to dissect off the wings (generally under water), taking with them just enough of the thorax to include the basal attachments of the tracheæ; then to place these wings upon the solidified glycerine jelly on the slide; then to lower upon the wings a heated cover glass, causing the jelly to melt enough to envelope the wings; and then to cool the mount speedily on a cake of ice, a marble slab, or in a draught of cold air. Rapid cooling is imperative, for in melted glycerine jelly the tracheæ soon become filled, and the smaller ones are then invisible.

It is imperative, also, that the wings be handled with care. Being simple sac-like structures, the tracheæ are almost free within them, and a slight pinch with forceps in the middle of the wing may throw all of its tracheæ out of place. It is better to lift the wing by its thoracic attachments or upon a section lifter.

Not every pupal wing is fitted for this study. Just before molting, and especially just before the last molting, the wing becomes so crumpled within its old sheath that the course of its tracheæ can be followed only with difficulty. Much time can be saved by the selection of the paler individuals for study.

It is obvious that one who has learned the homologies of the principal tracheæ of wings can easily determine the homologies of the wing-veins of the adult by the study of wings taken in the stage of development shown by Figs. 2 and 3. It should be remembered, however, that the determining of the homologies of these tracheæ necessitates the study of a large series of well-selected types. One is not warranted in arriving at conclusions in this matter from the study of a few representatives of a single order of insects.

During the past year we have studied in the manner indicated the wings of representatives of nearly all of the more important groups of winged insects, and have made several

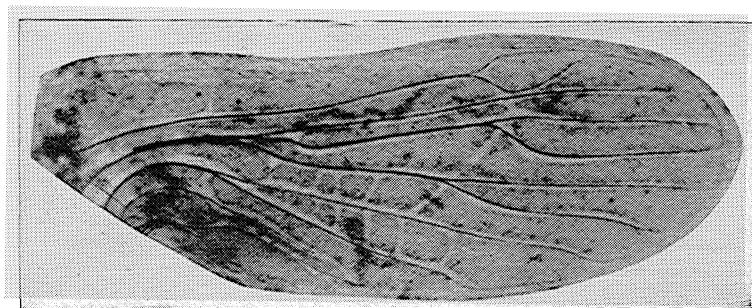


FIG. 2. — Fore wing of a nymph of *Nemoura*.

hundred photo-micrographs of them. We feel, therefore, that we have at hand sufficient data to warrant the conclusions regarding the homologies of the wing-veins that we purpose to offer.<sup>1</sup>

Although Figs. 2 and 3 will be discussed in detail in a subsequent chapter, we will give a few words of explanation here. These figures represent the wings of one side of a nearly mature nymph of a *Nemoura*, one of the genera of stone flies (Plecoptera). In making the preparations it was impracticable to remove all of the dirt adhering to the wings without danger of injuring them; this is often the case in preparing mounts of

<sup>1</sup> The most important gap in our series of observations is due to the fact that as yet we have been unable to procure pupæ of any of the Mecoptera. We would, therefore, be under great obligations to any one who would send us living pupæ of either *Panorpa* or *Bittacus*.

the wings of aquatic nymphs. The irregular blotches of dark color in the figures are due to this cause. The dark lines traversing the disk of the wing represent the tracheæ, and the pale bands the cuticular thickenings destined to form the wing-veins.

It will be observed that the principal veins are formed along the courses of tracheæ, while in most cases the cross-veins have no tracheæ within them. It will also be observed that the tracheæ extend in straight lines or in gentle curves, while in some cases the corresponding veins are much more angular.

It is evident from this that in the perfecting of a wing as an organ of flight the position of a vein in the adult may become

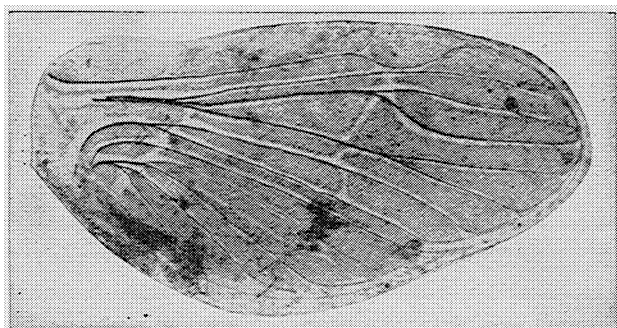


FIG. 3. — Hind wing of a nymph of *Nemoura*.

quite different from that of the corresponding trachea of the immature form. In other words, although there is no doubt that the courses of the principal wing-veins of primitive insects were determined by the position of the principal tracheæ of the wings, the wing-veins have been more or less modified to meet the needs of adult life; while at the same time the tracheæ of the immature wing, serving the purpose of respiration, and lying more or less free within the wing-sac, have not been forced to follow closely the changes in the cuticular thickenings of that sac.

The operation of this principle is shown only to a slight extent in the wings figured here. But when we study more highly specialized forms, it is seen that the divergence of these

two sets of structures is sometimes very wide, and must be taken into account in an interpretation of the characters presented by a wing.

While this increases the difficulty of determining the homologies of the wing-veins, it is often of great aid in taxonomic work, for it may afford an indication of the degree of divergence from a primitive type in the structure of a wing; and when a series of forms is studied the course of this divergence is often clearly indicated.

The figures also show that in some cases what appears as a single vein is formed about two closely parallel tracheæ. This is shown in the case of the bases of the second and third principal tracheæ, counting from the costal margin of the wing, the radial and medial tracheæ. This illustrates a fact of frequent occurrence, — that what appears to be a single vein may be formed by the coalescence of two primitive veins.

In these figures the tracheæ just mentioned, except one of them in the fore wing, appear not to extend to the base of the wing. This is due to the fact that in the preparations photographed the mounting medium had penetrated these tracheæ for a distance, rendering the basal portion of them invisible.

The figure of the hind wing illustrates also another way in which specimens may be injured during their preparation, and which may lead to a misinterpretation of them. In this wing the first branch of the first main trachea, the subcostal trachea, has been broken and moved out of place within the wing-sac. The normal position of this branch is well shown in the figure of the fore wing.

We will not go farther into the discussion of the technique of this method of study. Enough has been said to show that we have at hand a comparatively simple method of determining those questions of homologies of wing-veins that have sorely puzzled all investigators that have attempted to deal with them, and to indicate the nature of the material upon which we have based the conclusions that we purpose to offer in succeeding chapters of this paper.



## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER II.

#### *The Venation of a Typical Insect Wing.*

THERE are certain features of the venation of the wings of insects which occur in the more generalized forms of so large a proportion of the orders of this class that we are warranted in regarding them as typical of winged insects as a whole, and we are able to present a hypothetical type to which the wings of all orders may be referred.

This of course implies, what we believe to be the case, that all of the orders of winged insects have descended from a common winged ancestor. For it is not probable that had wings arisen more than once in this class that they should agree closely in their structural characteristics.

The recognition of the features of the wing venation that are common to the various orders of insects has been a matter of slow growth. Most writers on the subject have only attempted to work out the homologies of the principal veins within the limits of a single order; and thus have arisen the various systems of nomenclature of the wing-veins, which have done much to delay an appreciation of the uniformity of structure which really exists.

We will not take the space to trace out in detail the development of the idea that a uniform nomenclature of the wing-veins, based on homologies and, therefore, applicable to all orders, is possible. In 1870 Hagen attacked the problem in a paper, entitled "Ueber rationelle Benennung des Geäders in den Flügeln der Insekten."<sup>1</sup> But this essay apparently had little influence beyond calling attention to the importance of the subject. It was not till the appearance of the classic contribu-

<sup>1</sup> *Stettiner Entomologische Zeitung*, Bd. xxxi, pp. 316-320.

tion of Redtenbacher<sup>1</sup> that any great progress was made. This paper, with its numerous illustrations drawn from nearly all orders of winged insects, is really the starting point in the actual solution of the problem.

Unfortunately, however, Redtenbacher was misled by the erroneous theory of alternating convex and concave veins elaborated by Adolph.<sup>2</sup> The result was that, although Redtenbacher recognized the homologies of the main stems of the principal veins, he, in his efforts to apply this theory, was led into many serious errors.

Then Spuler<sup>3</sup> followed, and, basing his conclusions on a study of the tracheæ that precede the wing-veins, worked out the type of the lepidopterous wings. Unfortunately, Spuler overlooked the trachea that precedes the first of the principal veins, and began his numbering with the second principal vein, which he designated as vein I.

The next step in advance was made by the senior writer of the present series of articles. In a text-book of entomology<sup>4</sup> he worked out the homologies of the wing-veins in the Lepidoptera, Diptera, and Hymenoptera. In the preface of that book he said:

The principal features of the method of notation of wing-veins, proposed by Josef Redtenbacher, have been adopted. But as the writer's views regarding the structure of the wings of primitive insects are very different from those of Redtenbacher, the nomenclature proposed in this book is to a great extent original. The chief point of difference arises from the belief by the present writer that veins IV and VI do not exist in the Lepidoptera, Diptera, and Hymenoptera; and that, in those orders where they do exist, they are secondary developments.

But again, unfortunately, the work was not carried far enough. While the non-existence of the concave veins IV

<sup>1</sup> Josef Redtenbacher, *Vergleichende Studien über das Flügelgeäder der Insecten. Ann. des. k. k. naturhist. Hofmuseums*, Bd. i, 1886, pp. 153-232.

<sup>2</sup> G. Ernst Adolph, *Ueber Insectenflügel*, 1879.

<sup>3</sup> A. Spuler, *Zur Phylogenie und Ontogenie des Flügelgeäders der Schmetterlinge. Zeit. f. wiss. Zool.*, Bd. liii, 1892, pp. 597-646.

<sup>4</sup> J. H. and A. B. Comstock, *A Manual for the Study of Insects*. Ithaca, N. Y., 1895.

and VI of the Redtenbacher system was demonstrated for the orders named, no use was made of the wing venation in the other orders of insects; and his lack of definite knowledge on the subject made him willing to admit that these veins might exist as *secondary developments* in those orders with fan-like wings.

At last the time has come when we believe that we understand the homologies of the wing-veins in so large a proportion of the orders of insects that we are able to present a hypothetical type to which the wings of all orders may be referred. And this type includes not only the principal veins, but also the chief branches of these veins.

It should be borne in mind that our main object at this time is merely to trace the homologies of the wing-veins, to the end that a uniform nomenclature for all orders can be adopted, and also to enable us to make intelligent use in taxonomic work of the characters presented by them. We do not presume to say that we have definitely determined the peculiarities of the venation of the wings of the stem form from which winged insects have descended. We feel, however, that we have reached a sufficiently near approximation to this desired end to warrant our conclusions regarding the homologies of the wing-veins, and to enable us to commend a nomenclature for them which we believe can be accepted as final.

In designating the wing-veins they may be either named or numbered. The simplest method is, doubtless, to number them; and had the system which was proposed by Redtenbacher been based on a correct understanding of the primitive type, nothing better could be desired. But it was not; and, as several modifications of the Redtenbacher system are already in use, it seems doubtful if uniformity in numbering them could be soon brought about.

From the great mass of names that had been proposed for the principal wing-veins, Redtenbacher selected a set of terms, to the acceptance of which no objection has been urged. It seems, therefore, that the surest way to bring about uniformity of nomenclature is to give up the attempt to apply a set of numbers to the wing-veins, and to use the names adopted by

Redtenbacher. These names and the abbreviations of them, which we shall use in our text as well as in the figures illustrating it, are as follows:

Costa, <i>C.</i>	Media, <i>M.</i>
Subcosta, <i>Sc.</i>	Cubitus, <i>Cu.</i>
Radius, <i>R.</i>	Anal veins, <i>A.</i>

In designating the branches of the forked veins we have adopted the principle of numbering them proposed by Redtenbacher and combine the numbers with the abbreviations of the names of the veins. Thus, the first branch of radius is designated as *radius-one*; and for this term the abbreviation  $R_1$  is used.

In numbering the branches of the forked veins, *the same number is applied to homologous branches throughout the series of orders*. It is only in this way that the greatest use can be made of the characters presented by the wings in working out the phylogeny of groups.

But, in carrying out this plan, we have found that in certain orders, as, for example, the Neuroptera, there is a marked tendency towards the multiplication of the branches of some of the principal veins. It results from this that we find, in each of these orders, branches that have no true homologues in other orders, although in some cases analogous branches exist. As these supernumerary veins do not concern us while we are discussing the venation of the typical wing, we will postpone the consideration of them.

It frequently happens that the branches of a forked vein are reduced in number by the coalescing of two or more branches. In numbering such a compound branch the coalescence is indicated by the term applied to it. Thus, in very many insects, the second and third branches of radius coalesce throughout their entire extent, forming a single branch; this we designate as *radius-two-plus-three*, writing the term thus,  $R_{2+3}$ .

We will postpone for a time the discussion of the nomenclature of the cross-veins and of the cells of the wing, and proceed to a consideration of the hypothetical type to which we have referred.

There can be no doubt that the veins of the fore wings and of the hind wings are homodynamous. Any one that studies the subject much is impressed by this fact. A single diagram will be sufficient, therefore, to represent the venation of both pairs of wings of this type. Fig. 4 is such a diagram.

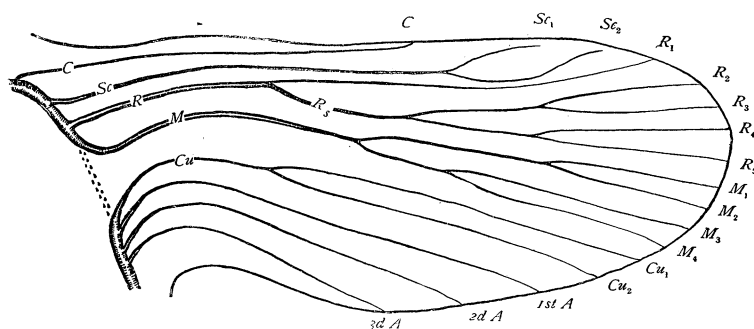


FIG. 4. -- Hypothetical tracheation of a wing of the primitive nymph.

As the wing of a nymph is much more instructive than a wing of an adult for the purpose of determining homologies, we represent this ideal wing in that stage of development in which the forming veins appear as light-colored bands and the tracheæ as dark lines. This stage in the wings of an actual nymph is well shown by the half-tone reproductions of photographs of the wings of a nymph of *Nemoura*, given in Chapter I (Figs. 2, 3).<sup>1</sup> In our hypothetical type we have represented only the tracheæ, which precede the forming veins.

By representing the wing of a nymph we are able to represent the basal connections of the tracheæ that precede the veins, and thus show which are principal veins and which are branches of them. This point has received very careful attention, a large number of nymphs and pupæ, representing nearly all of the orders of insects, having been examined especially for this purpose. Fortunately, this evidence confirms the conclusions reached by various writers who have studied only the wing-veins of the adult, and merely serves to remove any doubt there might have been regarding these conclusions.

Another point which can be brought out in this way is the

<sup>1</sup> *American Naturalist*, January, 1898. vol. xxxii, pp. 46, 47.

distinction between principal veins and cross-veins. For, although in certain highly specialized wings, as, for example, those of the Odonata, every cross-vein is preceded by a trachea, we have found that, as a rule, the secondarily developed cross-veins are not preceded by tracheæ. The figures of *Nemoura* in Chapter I illustrate this.

In the adult the front, or costal margin, of the wing is usually strengthened by a vein or a vein-like structure; this is designated as the *costa*. A study of immature wings shows that, although the costa usually extends more or less nearly to the apex of the wing, the costal trachea is, as a rule, greatly reduced. This reduction of the costal trachea has led to its being overlooked by previous writers, and to a denial of its existence by Brauer and Redtenbacher.<sup>1</sup> It is true that Brongniart figures what he believed to be the costal trachea in the nymph of a dragon fly;<sup>2</sup> but the structure which he represents is evidently the edge of the wing within the wing sheath of the nymph.

We have succeeded in finding the costal trachea in nearly all of the orders of winged insects, and have found that in widely separated forms, as in many Hemiptera and in the more generalized Hymenoptera, it extends nearly or quite to the apex of the wing. Further details regarding it will be given in the treatment of the separate orders. It is only necessary to state here that we have abundant evidence to support the view that the costa of the primitive insect wing resembled the other wing-veins in being preceded by a trachea, and that the origin and course of this trachea was probably very nearly as represented by *C* in Fig. 4. In the photographs of the wings of a nymph of *Nemoura*, reproduced in Chapter I, the costal trachea is not evident; but figures will be given of other Plecoptera in which this trachea is as distinct as any and extends to the middle of the wing.

The second of the principal veins of the wing is designated as the *subcosta*. This extends more or less nearly parallel with the costa and but a short distance from it. In those orders

<sup>1</sup> *Zool. Anz.*, Bd. xi, 1888, pp. 443-447.

<sup>2</sup> *Rech. sur les Insectes Fossiles*, Pl. viii, Fig. 1, a.

where there are many wing-veins it gives off numerous small branches to the costa; in the orders where there are few wing-veins it appears in the adult to be an unbranched vein. But a study of the subcostal trachea in nymphs and in pupæ shows that it is forked in at least several widely separated orders; we have, therefore, represented it so in our type (Fig. 4,  $Sc_1$  and  $Sc_2$ ). In adult wings the branches of the subcosta are usually either wanting or appear as cross-veins. In those orders in which the wing is corrugated the subcosta lies at the bottom of a furrow, which stiffens the costal edge of the wing.

The third vein is the *radius*. This is the most prominent vein in the wing; and it is the one which, from the great variety of its modifications, offers more often than any other vein obvious characters of use in taxonomic work. In spite of the wide differences of form of this vein in the different orders, it is now clear to us that these various forms have all been derived from a type which still exists, but slightly modified, in the more generalized Trichoptera, Mecoptera, Diptera, and Lepidoptera, and in certain genera of several other orders. In its typical form this vein is five-branched (Fig. 4,  $R_1-R_5$ ). The main stem of the vein separates into two divisions; the first of these is simple and is more or less nearly a direct continuation of the main stem — this is *radius-one* ( $R_1$ ); the second of the principal divisions of radius is typically four-branched, and on account of the frequency of the necessity of making reference to it a special name has been applied to it, the *radial sector* ( $R_s$ ). The radial sector separates into two divisions ( $R_{2+3}$  and  $R_{4+5}$ ); and each of these again separates into two divisions, the former into *radius-two* ( $R_2$ ) and *radius-three* ( $R_3$ ), and the latter into *radius-four* ( $R_4$ ) and *radius-five* ( $R_5$ ).

The vein occupying the center of the wing is the *media* ( $M$ ). In those orders in which it retains most nearly its primitive form it is usually three-branched; but the fact that in the more generalized members of several widely separated orders it is four-branched leads us to believe that it was four-branched in the stem form of winged insects. The branches are designated as *media-one* ( $M_1$ ), *media-two* ( $M_2$ ), *media-three* ( $M_3$ ) and *media-four* ( $M_4$ ), respectively.

The fifth principal vein is the *cubitus* (*Cu*); this vein separates into two branches, — *cubitus-one* (*Cu<sub>1</sub>*) and *cubitus-two* (*Cu<sub>2</sub>*).

Between the cubitus and the anal margin of the wing there are typically three veins; these are commonly termed the anal veins. We will distinguish them as the *first anal* (*1stA*), the *second anal* (*2dA*), and the *third anal* (*3dA*), respectively, the first anal being the one nearest to the cubitus.

The first anal vein is generally simple; but in those orders where the anal area of the wing is expanded the second and third anal veins become separated into many branches, which form the supports of the fan-like portion of the wing.

Before leaving the discussion of this hypothetical type it seems necessary to say a little regarding the basal connections of the tracheæ that precede the wing-veins. In what appears to us to be the most generalized type, the tracheæ that supply the wing with air arise from two distinct trunks, as shown in Fig. 4. The first of these trunks is a branch of the dorsal longitudinal trachea of the thorax; the second, of the ventral longitudinal trachea. This type exists in all Plecoptera that we have examined and in certain cockroaches; we have not found it elsewhere.

The two groups of wing-tracheæ thus formed may be designated as the *costo-radial group* and the *cubito-anal group*, respectively. When the two groups are distinct, the trachea that precedes the media is a member of the the costo-radial group.

In most insects there has been developed a transverse trachea connecting these two groups of tracheæ; the position of this *transverse basal trachea* of the wing is indicated in the figure by dotted lines. Frequently the transverse basal trachea is indistinguishable from the two main trunks which it connects, the three forming a single, continuous, transverse trachea, from which arise all of the wing tracheæ. All of the stages of this development have been found by us within the Orthoptera.

When a transverse basal trachea is formed, the medial trachea (*i.e.*, the trachea that precedes media) tends to migrate along it towards the cubito-anal group of tracheæ, and often becomes united with that group. This is well shown in certain Orthoptera and in the Hemiptera. In some cases the base of



the radial trachea tends to follow the base of the medial in its migration along the transverse basal trachea towards the cubito-anal group (*Acrididæ*).

We have found no indication that the formation of a transverse basal trachea and the subsequent migration along it of the base of the medial trachea is influenced at all by the flight function of the wing, as the arrangement of the wing-veins does not appear to be modified by it. It should be remembered that the transverse basal trachea and the bases of the wing tracheæ are within the thorax of the adult insect, and are thus beyond the influence of the migrations of the wing-veins.

It is probable that these changes have to do with improving the air supply of the wing; but we have not sufficient data, as yet, to warrant a definite statement on this point. The important thing for the purposes of the present discussion is that one must know of this tendency on the part of the medial trachea to migrate along the transverse basal trachea in order to be able to recognize it in its various positions.

ENTOMOLOGICAL LABORATORY,

CORNELL UNIVERSITY, December, 1897.



# THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

## CHAPTER III.

### *The Specialization of Wings by Reduction.*

#### I. INTRODUCTION.

THE recognition of certain features of the venation of the wings of insects which occur in the more generalized forms of a large proportion of the orders of this class has enabled us to present a hypothetical type to which the wings of all orders may be referred. A detailed discussion of the features of this

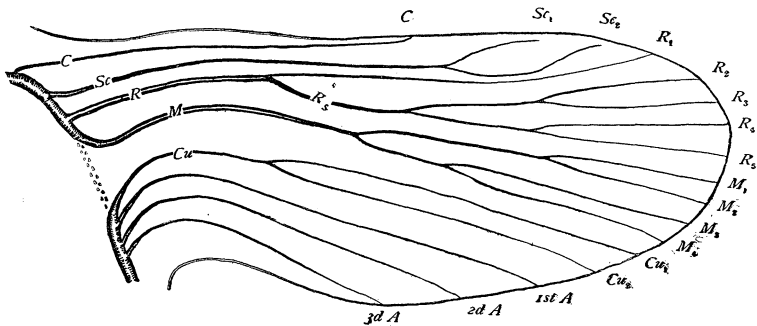


FIG. 5.—Hypothetical type.

type has already been given; the figure representing it is repeated here (Fig. 5) in order that it may be easily compared with figures of actual wings. It represents the supposed arrangement of the tracheæ in a wing of the nymph of the primitive winged insect. By omitting the basal part, the figure will also serve to show the number and arrangement of the longitudinal wing-veins of the adult.

It will be seen at a glance that this hypothetical type differs from the great majority of living insects in the possession of a larger number of wing-veins than is characteristic of them; it also differs, and in a more striking degree, from most of the

insects of the Linnean order Neuroptera in having a much smaller number of wing-veins than is possessed by them.

These differences indicate two different methods of specialization by which this primitive type has been modified: the one, specialization by reduction; the other, specialization by addition.

We postpone any farther reference to the latter method of specialization and confine our attention in this place to a study of some of those forms in which a tendency to modify the primitive type by a reduction in the number of wing-veins is evident.

A reduction in the number of wing-veins takes place in two ways: first, by atrophy of veins; second, by the coalescence of two or more adjacent veins.

The first method is illustrated in most of the orders where a reduction in the number of wing-veins has taken place by the atrophy, more or less complete, of one or more of the anal veins; this is correlated with a reduction in the extent of the anal area. This method is also illustrated in certain cases where there is no apparent reduction of the area of the wing from which the vein has disappeared. The most familiar illustrations of this occur in the Lepidoptera. In this order, as is well known, the main stem of the media disappears in many families; and in the geometrid moths of the family Eunomidæ, the second branch of this vein is also lost.

The second method of reduction — that is, by coalescence — takes place in all of the orders in which the number of wing-veins is less than in the typical wing. This also takes place in two ways: first, the point at which two veins separate occurs nearer and nearer the margin of the wing, until finally, when the margin is reached, a single vein remains where there were two before; second, the tips of two veins may approach each other on the margin of the wing until they unite, and then the coalescence proceeds towards the base of the wing. The former is a coalescence extending outward; the latter, a coalescence extending inward. Examples of the former are common in all of the orders discussed in this chapter; illustrations of the latter are most easily observed in the Diptera.

The typical arrangement of the wing-veins is often modified, also, by an anastomosis of two veins; that is, two veins will come together at some point more or less remote from their extremities and merge into one for a greater or less distance, while their extremities remain separate. This is illustrated in *Nemoura* (Fig. 8), where veins  $Sc_2$  and  $R_1$  anastomose.

In the preceding chapter we suggested a nomenclature of the principal wing-veins and of their chief branches, which is applicable to all of the orders of winged insects. At that time nothing was said regarding the cross-veins; for it seems hardly

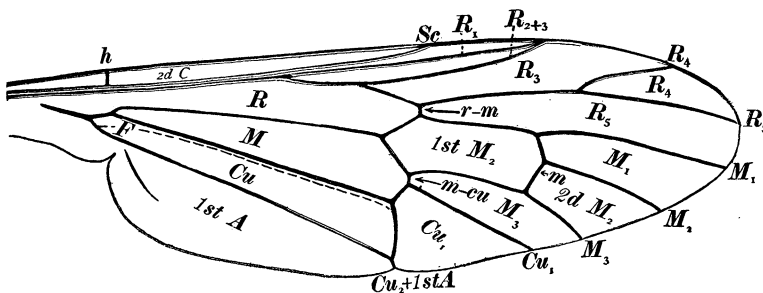


FIG. 6. — Wing of a Leptid, showing cross-veins and cells.

practicable to propose a nomenclature of these based on homologies which shall have an equally general application. This arises from the fact that in those orders where the number of wing-veins is greatly increased, the primitive cross-veins, if such exist, are in most cases indistinguishable from those that have been developed secondarily.

But when we examine the wings of those orders in which the tendency is towards a reduction in the number of wing-veins, we find that there are a few cross-veins which are so constant in their position and which occur in so many widely separated groups that they are evidently homologous. As the number of these is small, we propose to designate them by names, as follows:

*The humeral cross-vein.* This is a single cross-vein extending from the subcosta to the costa near the humeral angle of the wing (Fig. 6, *h*). This is the most constant of all of the cross-veins.

*The radio-medial cross-vein.* This is a cross-vein extending from radius to media, usually near the center of the wing, and is designated by the abbreviation *r-m*. When in its typical position, this cross-vein extends from  $R_{4+5}$  to  $M_{1+2}$ ; this results in one end being opposite cell  $R_3$  and the other end opposite cell 1st  $M_2$ . The cells are defined a little later.

*The medio-cubital cross-vein.* This is a cross-vein extending from media to cubitus, usually near the center of the wing. It is designated by the abbreviation *m-cu*. When in its typical position this cross-vein extends from a point near the base of  $M_{3+4}$  to a point near the base of  $Cu_1$ .

*The medial cross-vein.* This is a cross-vein extending from media-two ( $M_2$ ) to media-three ( $M_3$ ); this is designated by the abbreviation *m*. The presence or absence of this cross-vein is often a character of considerable taxonomic importance.

*The arculus.* In many insects there is what appears to be a cross-vein extending from radius to cubitus near the base of the wing. This has been termed the arculus by writers on the

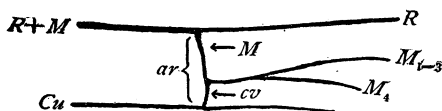


FIG. 7. — The arculus, diagrammatic.

Odonata, and we propose to extend the use of the term to all orders in which there is a similar arrangement of the veins in this part of the wing.

The arculus is designated by the abbreviation *ar*. Usually when the arculus is present the media appears to arise from it. The fact is, the arculus is compound, being composed of a section of the media and a cross-vein. The structure of this part can be clearly seen in the Odonata (Fig. 7).

In descriptions of wings it is often desirable to refer to one or more of the cells. It is necessary, therefore, to have a nomenclature of the cells of the wing, as well as of the wing-veins. Certain of the cells have received special names; but as no effort has been made by those proposing them to trace the homologies of the cells beyond the limits of a single order, the names proposed are not available for our present purposes. A single example will serve to illustrate this. We find the term

*disca* cell used in descriptions of Lepidoptera, Diptera, Trichoptera, and Corrodentia (Psocidæ), but in no two of these orders is it applied to the same cell.

Having named the wing-veins, the simplest possible method of designating the cells of the wing is to apply to each the abbreviation of the name of the vein that forms its cephalic (front) margin. It should be borne in mind, however, that by modifications of the typical arrangement of the wing-veins, a vein that normally forms the cephalic margin of a cell may apparently bear a very different relation to it; and this must be taken into account if we are to apply the same term to homologous cells throughout the insect series.

The cells of the wing fall naturally into two groups: first, those on the basal part of the wing; and second, those nearer the distal end of the wing. The former are bounded by the principal veins; the latter, by the branches of the forked veins; a corresponding distinction is made in designating the cells. Thus the cell lying behind the main stem of radius and on the basal part of the wing is designated as cell  $R$ ; while the cell lying behind radius-one is designated as cell  $R_1$ .

It should be remembered that the coalescence of two veins results in the obliteration of the cell that was between them. Thus when veins  $R_2$  and  $R_3$  coalesce, as in *Leptis* (Fig. 6), the cell lying behind vein  $R_{2+3}$  is cell  $R_3$  and not cell  $R_{2+3}$ , cell  $R_2$  having been obliterated.

When one of these principal cells is divided into two or more parts by one or more cross-veins, the parts may be numbered, beginning with the proximal one. Thus in *Leptis* (Fig. 6), cell  $M_2$  is divided by the medial cross-vein into two parts, which are designated as 1st  $M_2$  and 2d  $M_2$ , respectively.

The application of this system of naming the cells of the wing is an easy matter in those orders where the wings have few veins; but in those orders where many secondary veins are developed it is more difficult of application. In the latter case we have to do with *areas* of the wing rather than with separate cells. Thus, for example, it will be shown later that in certain Neuroptera the area  $R_2$  is divided by several longitudinal veins, which are connected by many cross-veins, the area  $R_2$  (which

is strictly homologous with cell  $R_2$ ) being composed of a large number of secondary cells.

The wings of comparatively few insects present a flat surface; in most cases we find that the membrane is thrown into a series of folds or corrugations. This corrugating of the wing in some cases adds greatly to its strength. This is well shown by the wings of dragon flies; and in most orders the costal margin of the wing is strengthened by a fold between costa and radius, the *subcostal fold*. In other cases, the corrugations are the result of a folding of the wing when not in use; this is well shown in the anal area when this part is broadly expanded.

It rarely happens that there is occasion to refer to individual members of either of these classes of folds, except, perhaps, to the one that has just been designated as the subcostal fold. But there are three other furrows which it is necessary to designate, as we shall have frequent occasion to refer to them. These we term the anal furrow, the median furrow, and the nodal furrow, respectively. They may be defined as follows:

*The anal furrow.* This is a longitudinal furrow which is usually between the cubitus and the first anal vein (Fig. 6, *F*). It has been referred to by many writers, but the variableness of its position has not been pointed out.

*The median furrow.* This is a longitudinal furrow which is usually between radius and media. It is well marked in many of the Hemiptera, where it separates the embolium from the remainder of the corium; and in the Hymenoptera its course is marked by a series of weak spots (bullæ) in certain veins.

*The nodal furrow.* This is a transverse suture beginning at a point in the costal margin of the wing, corresponding to the nodus of the Odonata and extending towards the inner margin of the wing. It crosses a varying number of veins in different orders of insects.

The furrows of the wing are in no sense homologous or even analogous to veins. More than this, as will be shown repeatedly, the relative positions of the furrows and of the wing-veins are not constant; for it frequently happens that the course of a vein has been so modified that it crosses the line of a furrow and the relative positions of the two are thus reversed. If this fact



had been understood by Adolph we would have been spared his misleading theory of alternating concave and convex veins.<sup>1</sup>

## II. THE VENATION OF THE WINGS OF CERTAIN PLECOPTERA.

If we leave out of consideration the anal area, that portion of the wing traversed by the anal veins, we will find that in nearly every case each order of insects is characterized by either a reduction or a multiplication of the wing-veins; in certain orders the tendency is in one direction, while in others it is in the opposite. But either of these tendencies may be correlated with a similar tendency in the anal area or with the opposite one. In this chapter we purpose to point out the ways in which the primitive type of wing venation has been modified in representatives of several of the orders where a reduction in the number of wing-veins in the preanal area has taken place.

In the order Plecoptera, or stone flies, we find that, although in most genera the anal area of the hind wings has been expanded and the number of anal veins increased, in the preanal areas of both wings the number of wing-veins has been increased in certain genera and reduced in others; and we cannot say that either of these tendencies has yet attained the ascendancy within this order.

This fact, taken in connection with the generalized condition of the basal attachments of the tracheæ of the wings, already pointed out, leads us to believe that the Plecoptera as a whole depart less widely from the primitive winged insect than do the living representatives of any other order.

In this place, we have to do only with those Plecoptera in which a reduction in the number of wing-veins in the preanal area of the wing has taken place. Of these, the genera *Nemoura* and *Tæniopteryx* are taken as examples. And we use, for the purposes of this study, wings of nymphs taken at a stage when the forming wing-veins appear as light-colored bands and the tracheæ, about which they are formed, as dark lines.

<sup>1</sup> G. Ernst Adolph, Ueber Insectenflügel. *Nova Acta der ksl. Leop.-Carol. Deutschen Akademie der Naturforscher.*, Bd. xli, pp. 215-251. 1879.

In the nymph of *Nemoura* (Fig. 8) we have not observed a costal trachea. The subcosta is forked in the typical manner, and vein  $Sc_2$  anastomoses with vein  $R_1$ . The radius is reduced, the radial sector being only two-branched; it is probable that this reduction came about by the coalescence outward of vein  $R_2$  with  $R_3$  and of vein  $R_4$  with  $R_5$ . The media is reduced in a similar way. The cubitus is typical, but in the fore wing sev-

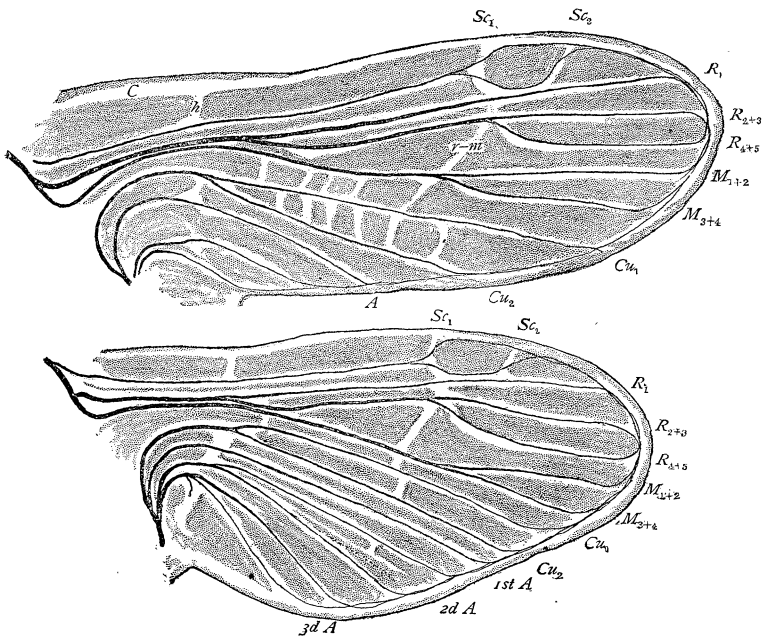


FIG. 8.—Wings of *Nemoura*, nymph.

eral cross-veins have been developed between its branches, and also between it and the media; the strengthening of this region of the fore wing is quite characteristic of the Plecoptera. The anal veins are typical in the fore wing, but in the hind wing the second and third anal veins are each forked.<sup>1</sup>

<sup>1</sup> There is a striking similarity between the anal areas of the Plecoptera and the Orthoptera; throughout both these orders the first anal vein remains simple in both wings, but the second and third anal veins are forked when this part of the wing is expanded.

The wings of a nymph of *Tæniopteryx* (Fig. 9) show a slightly different modification of the type. The costal trachea is well preserved. The subcosta is typical. The radial sector is reduced

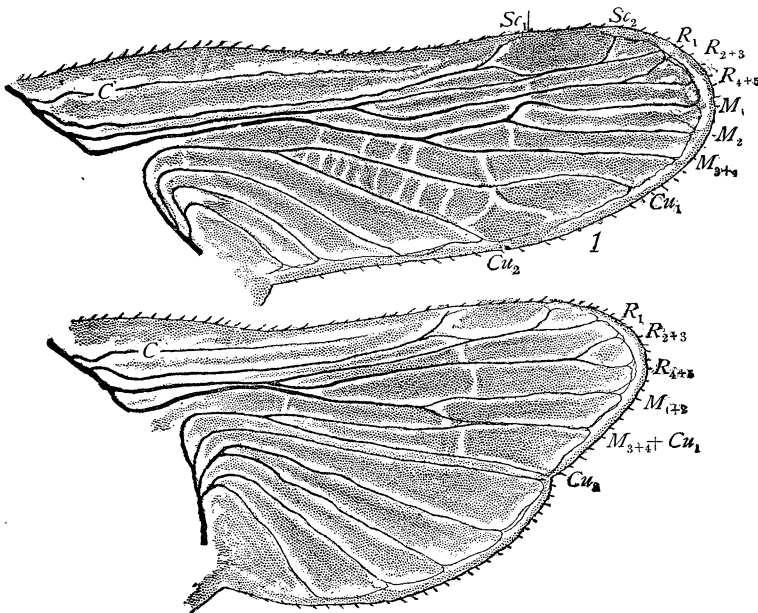


FIG. 9. — Wings of *Tæniopteryx*, nymph.

even more than in *Nemoura*, the coalescence of veins  $R_{2+3}$  and  $R_{4+5}$  having extended to near the margin of the wing; the carrying of this process a little farther would reduce the radial

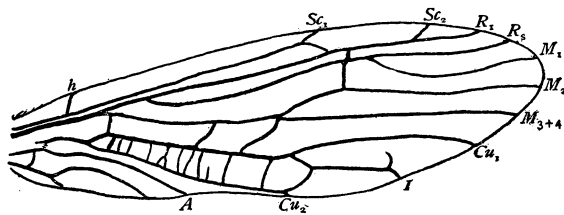


FIG. 10. — Wing of *Tæniopteryx*, adult.

sector to an unbranched condition, which is what has happened in some species of this genus (Fig. 10). The media is three-branched in the fore wing and two-branched in the hind wing, but in the hind wing vein  $M_{3+4}$  coalesces with vein  $Cu_1$ . The

cubital trachea is typical in both wings, and the anal veins are quite similar to those of *Nemoura*.

There are two points of especial interest in the fore wing of this insect, both showing the importance of ontogenetic study in determining the homologies of wing-veins.

First, it is evident that, correlated with the great reduction of the radial sector, vein  $M_1$  of the fore wing, which remains distinct from vein  $M_2$  in this genus, has come to perform the function that is performed by vein  $R_{4+5}$  in *Nemoura*; and, as a result, it has assumed a similar position. So great is the similarity that one who studied only the wings of the adult *Tænipteryx* would be certain to mistake vein  $M_1$  for a branch of the radial sector. A glance at Fig. 10, which represents the fore wing of the adult of another species of this genus, will make this more evident. If the object in view were merely to number the wing-veins, it may be that a mistake of this kind would not be serious; but when the object is to determine the relationships of allied forms, such a mistake would surely lead one astray.

The second point illustrates specialization by addition, and it is anticipating somewhat to allude to it here. It will be observed that in Fig. 10 a vein which ends in the margin of the wing midway between veins  $Cu_1$  and  $Cu_2$  is labeled 1. This is what we shall define later as the first accessory cubital vein. A reference to Fig. 9 will show that, although this vein has the same appearance as other longitudinal veins in the adult, it is not preceded by a trachea in the nymph, but, like the cross-veins, is formed secondarily. This is an illustration of the beginning of a process which is carried to a great extent in those insects that have wings with many wing-veins, and which will be described in more detail later.

It will be seen from these two illustrations that a study of the ontogeny of the wings opens a fruitful field to one engaged in a study of the genetic relationships of winged insects.

### III. THE VENATION OF THE WINGS OF *PSOCUS*.

The determining of the homologies of the wing-veins in *Psocus* and allied genera is a problem that has sorely puzzled all who have worked upon it; and it has remained till now

unsolved, although it has been attacked by such writers as Hagen, McLachlan, and Kolbe.

But when it is approached by the ontogenetic method the difficulties vanish, and it is hardly necessary to do more for its solution than to refer to the accompanying figures representing

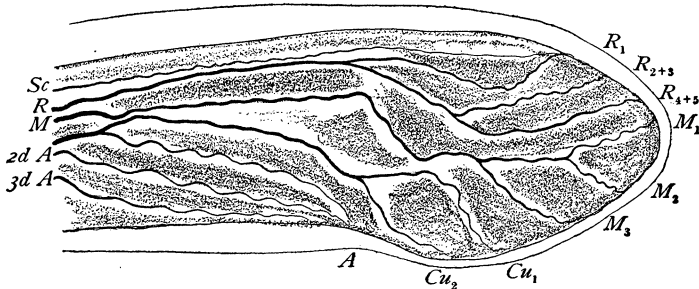


FIG. 11. — *Psocus*, fore wing of a nymph.

three stages in the development of the fore wing of *Psocus venosus*. When one understands this wing, the working out of the homologies in the hind wing, which is more reduced, and in the wings of other genera is a comparatively simple matter.

Fig. 11 represents the wing of a nymph which was not yet full grown. The lettering of the figure indicates the homologies

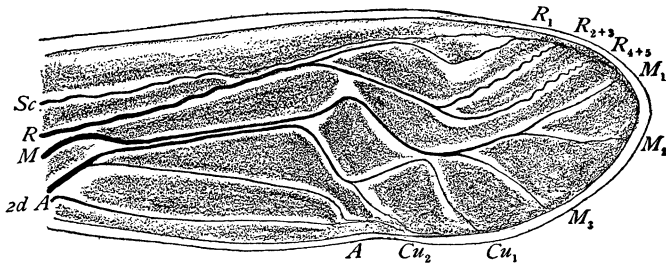


FIG. 12. — *Psocus*, fore wing of a full-grown nymph.

of the tracheæ. The formation of the wing-veins has begun, but in most cases the outlines of these are vague. It will be observed that the wing is much smaller than the enveloping sheath.

Fig. 12 represents the wing of a full-grown nymph. Here the forming veins are much more definite in outline, and there is no difficulty in tracing the venation of the adult wing. The

costal trachea is preserved for only a short distance; the subcostal trachea extends far beyond the end of the forming vein; and for a considerable part of its course is within the light band that is to form the radius; the radial sector has been reduced to two branches; and only three branches of the media remain. The most striking features of this wing are the coalescence of media and cubitus, which is shown by the two tracheæ being

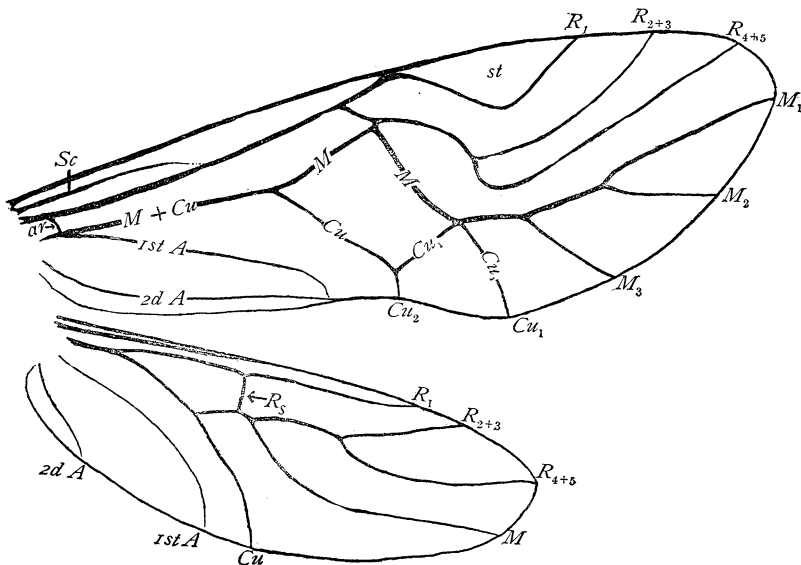


FIG. 13. — *Psocus*, wings of an adult.

closely parallel for a considerable distance within a single vein, and the zigzag course of media, which is easily determined by following the course of the medial trachea. Neither of these features is so well marked in the less mature wing. The first anal vein coalesces with cubitus at the base. The second anal vein has moved nearer to the margin of the wing. And the third anal trachea is no longer visible.

The wings of the adult are represented by Fig. 13. A remarkable feature of these wings is that, although they are braced in every direction, there is not a single cross-vein present, except an arculus which is formed of the base of the media; the bracing is accomplished by the zigzag courses of the prin-

cipal veins. This, however, is not true of all psocids. In some the bend in the media does not reach the radial sector, and the two are connected by a radio-medial cross-vein.

The margin of the adult wing is tubular throughout, there being what has been termed by writers on the *Diptera* an ambient vein. The costal and anal portions of this doubtless represent the costa and third anal veins, respectively, although the corresponding tracheæ are apparently lost. The distal portion of this ambient vein was preceded by the anastomosing tips of all of the veins, as is shown in the figures of the nymph wings. In the fore wing the tip of the subcosta coalesces with the radius; in the hind wing it coalesces with the costa. In the fore wing a large stigma is developed in an angle of vein  $R_1$ ; and in both wings the anal furrow coincides with the first anal vein.

#### IV. THE VENATION OF THE WINGS OF A CICADA.

A study of the wings of *Hemiptera* reveals remarkable departures from the primitive type of wing venation. So great are these that, at first, one sees very little in common between the wings of a bug and those of insects of any other order. We were filled with delight, therefore, when we found within this order, preserved almost unchanged, what we had come to regard, from a study of other orders, as the primitive type of wing venation.

The conservative *Hemiptera* that retain most perfectly the fashions of ancient times, so far at least as concerns the venation of the wings, are the cicadas. But the slightness of the changes that have taken place is not obvious if one studies only the wings of the adult; for in this stage there is a massing of several veins along the costal margin of the wing, and the cross-veins have the same appearance as the branches of the primary veins.

In the wings of a young nymph, on the other hand, the tracheæ that precede the primary veins are not massed as they are later, and in the older nymph where the forming veins appear as pale bands the cross-veins contain no tracheæ.

In the wing of a nearly mature nymph (Fig. 14) the costal trachea extends nearly to the apex of the wing. The subcostal trachea is also prominent, but it is not forked. The radius is reduced to a three-branched condition. The media is typical. So, too, is the cubitus. The first anal trachea coalesces with the cubital trachea for a considerable distance. The second and third anal tracheæ are also united at the base, and the forming veins appear as pale bands.

The important departures from the primitive type are two: first, the coalescence of the first anal vein with the cubitus. This results in the anal furrow of the adult lying between the first and second anal veins; but these two are closely opposed

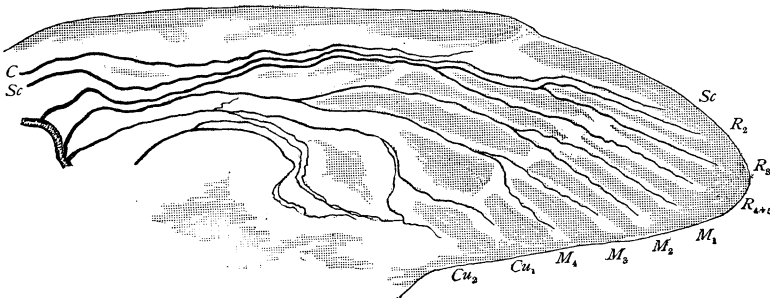


FIG. 14. — Cicada, fore wing, mature nymph.

in the fore wing of the adult, except for a short distance at the base of the wing, so that they appear as a single vein along the line of the furrow. The study of the wings of an adult which was killed at the moment of emergence from the nymph skin, and in which the tracheæ of the wings are distinctly visible within their corresponding wing-veins, has materially aided us in determining the relation of the anal furrow to the adjacent veins. It may be said in this connection that the coalescence of the first anal vein with the cubitus is a common occurrence in several of the orders.

A more striking departure from the primitive type is the reduction of the radius. For a long time we were unable to decide in what manner this had taken place. The usual mode of reduction of this vein is by the coalescence outward of the two branches of each half of the radial sector, leaving the



sector two-branched and the vein as a whole three-branched, as in *Nemoura* and in *Psocus*. But in these cases the intermediate branch of the radius arises from the posterior one of the three; in *Cicada*, on the other hand, the intermediate branch arises from the anterior one of the three (Fig. 14).

It was not till we succeeded in obtaining a very young nymph of *Cicada* that this question was definitely settled. In the fore wing of this nymph (Fig. 15) the radial trachea is five-branched; and the only departure from the typical mode of branching is

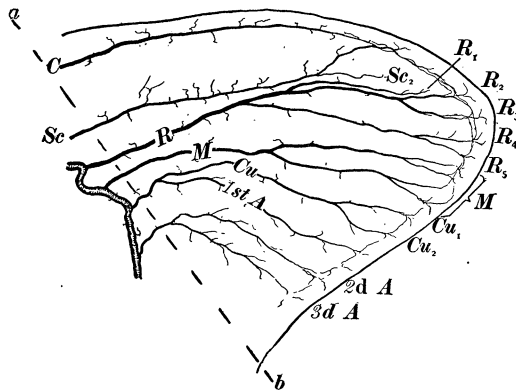


FIG. 15. — *Cicada*, fore wing, young nymph.

that the branch which corresponds to vein  $R_1$  coalesces for a short distance with the one corresponding to the anterior half of the radial sector.

It will be observed that in this part of the wing the subcostal trachea closely approaches the radial. This crowding of the radial trachea by the subcostal is doubtless the explanation of the pushing outward of the point of separation of the trachea  $R_1$  and of the complete atrophy of this trachea in the later stages of this insect, which results in the non-development of vein  $R_1$ .

We have discussed this matter at some length, not merely to show the close correspondence of the tracheation of the wing of the young nymph to our hypothetical type, but also to point out the course by which has been reached one of the most characteristic features of the venation of the wings of Hemiptera, that is, the complete absence of vein  $R_1$ .

From a study of the two nymph wings figured here, it is an easy matter to trace the homologies of the veins and cells of

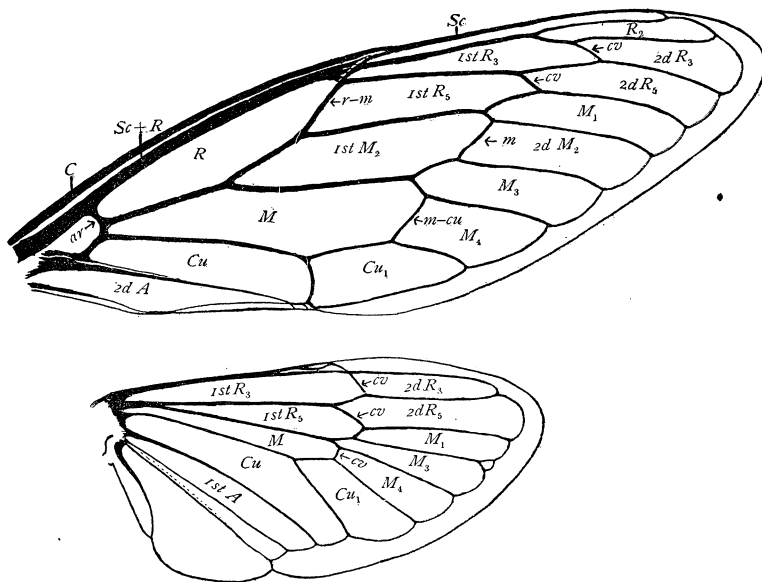


FIG. 16. — Cicada, wings of adult.

the fore wing of the adult; these are indicated by the lettering of this part in Fig. 16.<sup>1</sup> The more difficult points are eluci-

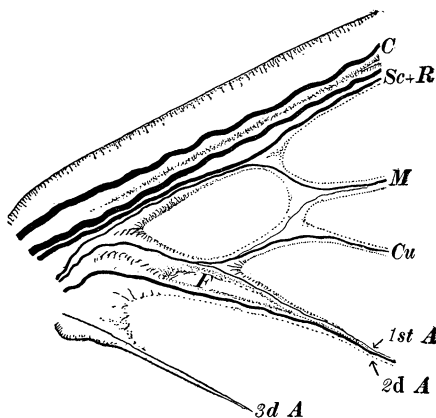


FIG. 17. — Cicada, base of fore wing.

<sup>1</sup> In those cases where the veins are not numbered, their homologies are indicated by the numbering of the cells behind them.

dated by Fig. 17, which represents the base of the fore wing of the adult, and Fig. 18, which represents the region of the nodal furrow of the same wing. These figures are based on a study of the recently emerged adult, already referred to. We

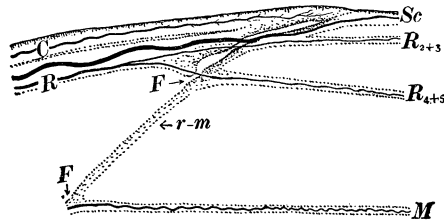


FIG. 18. — Cicada, nodal furrow of the fore wing.

wish to call attention especially to the coalescence of subcosta and radius from the base of the wing to a point near the nodal furrow, as this is a feature which occurs in a large proportion of the families of the Hemiptera.

The changes that have taken place in the hind wing of Cicada are much greater than those of the fore wing, and it would be

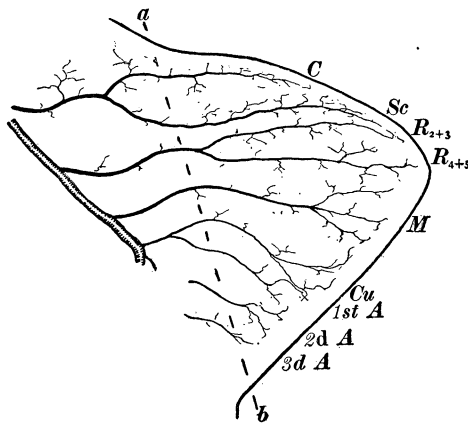


FIG. 19. — Cicada, hind wing, young nymph.

exceedingly difficult to understand them without the aid of ontogenetic study. But a careful comparison of the hind wing of a young nymph (Fig. 19) and the base of the hind wing of the recently emerged adult (Fig. 20) has cleared up the doubtful points.

In comparing the wings of nymphs, and especially of young nymphs, with those of the adult, it will be found that the growth of the basal part of the wing proceeds more rapidly at first than does that of the distal portion. This is shown by the fact that the branching of the branched tracheæ occurs much nearer the outer margin of the wing in the nymph than does the branching of the corresponding veins in the adult.

The difference is not so great, however, as appears at first sight, for only a part of what is represented in Fig. 19 corresponds to the wing of the adult. The dotted line *a-b* indicates

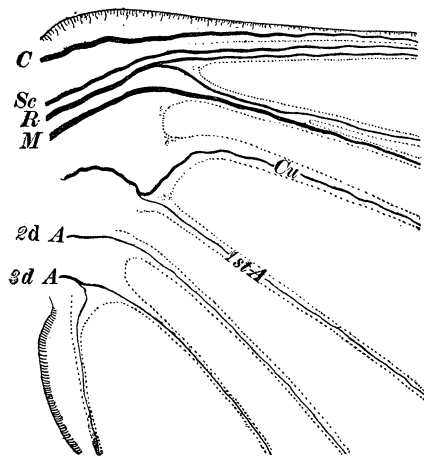


FIG. 20. — Cicada, base of hind wing.

approximately the line along which the hinge of the wing of the adult is formed. In Fig. 15, the line *a-b* represents the corresponding part in the fore wing.

By comparing Figs. 15 and 19 it will be observed that the forking of the radial trachea takes place much nearer the hinge line in the hind wing than it does in the fore wing. Upon this fact depends the most striking difference in the venation of the fore and hind wings of the adult.

In the fore wing we found that subcosta and radius coalesce to a point near the nodal furrow. But in the hind wing it is only the anterior half of what is left of the radius after the loss of vein *R*<sub>1</sub> that coalesces with the subcosta. The posterior half,

vein  $R_{4+5}$ , separates from vein  $R_{2+3}$  very near the base of the wing, and coalesces with the media for a short distance, after which it traverses the wing as a separate vein. A result of this is that while the 1st cell  $R_3$  of the fore wing lies beyond the nodal furrow, in the hind wing it reaches the base of the wing; and the 1st cell  $R_5$  occupies a similar position. A study of the base of the hind wing of the recently emerged adult (Fig. 20) confirms these conclusions.

Other features of interest in the hind wing are the following: The media is only three-branched as a rule, but in some specimens there is a small remnant of cell  $M_2$ . The first and second anal veins are widely separate, and the third anal vein is forked.

In the course of the development of the wing of *Cicada* there is an excellent illustration of the migration of the base of the medial trachea, which was referred to at the close of Chapter II. In the young nymph of *Cicada* (Fig. 15) the medial trachea arises from the transverse basal trachea midway between the radial and cubital tracheæ. In the mature nymph (Fig. 14) the base of the medial trachea has reached the cubital trachea.

In tracing the homologies of the tracheæ of the wings, it is very important that this migration of the base of the medial trachea be kept in mind. For while in the more generalized forms where there is no basal transverse trachea (Plecoptera and certain Blattidæ) the medial trachea belongs to the costo-radial group of tracheæ, whenever a basal transverse trachea is present the medial trachea either arises from it or is a member of the cubito-anal group. The ontogeny of *Cicada* gives conclusive evidence of this migration. In all mature nymphs of Hemiptera that we have examined the migration has taken place, the medial trachea being a member of the cubito-anal group.

#### V. THE VENATION OF THE WINGS OF HETEROPTERA.

In *Cicada* we found the most generalized condition of the wings that exists in the hemipterous insects that we have studied, and it is hardly to be expected that a more generalized

form will be found among the living representatives of this order. We have now to consider modifications of this type in representatives of the suborder Heteroptera.

In our studies of Heteroptera we have examined nymphs of the following families: Notonectidæ, Nepidæ, Belostomidæ, Reduviidæ, Nabidæ, Capsidæ, and Pentatomidæ. Of these there is no doubt that the most generalized condition of wing venation is found in the family last named, but further studies in other families may reveal a still more primitive type.

Fig. 21 represents the tracheation of the fore wing of a

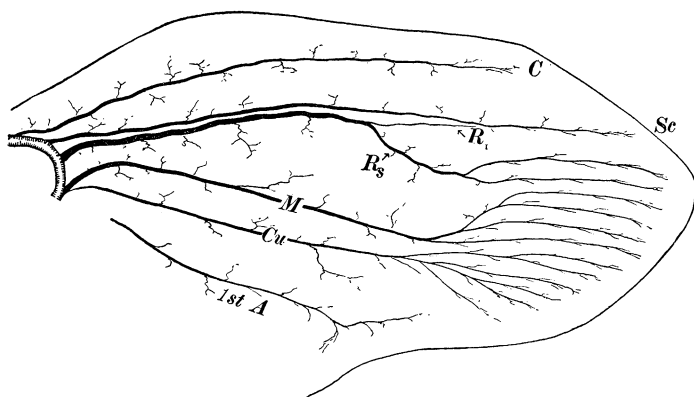


FIG. 21. — A Pentatomid, fore wing, nymph.

Pentatomid nymph. In this wing the costal trachea is well preserved. The subcostal and radial tracheæ are closely approximate in the basal half of the wing; in the distal half of the wing the subcostal trachea traverses that part of the wing which would be traversed by trachea  $R_1$  were it well developed and in its typical position; but it is reduced to a rudimentary condition. It is evident that a supplanting of  $R_1$  by the subcosta takes place here, as in Cicada. The trachea that precedes the radial sector has its characteristic bend at the base, and is two-branched. The medial trachea is typical, that is, four-branched. The cubital trachea is six-branched; it is evident that a specialization by addition has taken place here. Only a single anal trachea has been preserved.

The hind wing of the same nymph (Fig. 22) presents a very similar arrangement of tracheæ, except in a greater reduction of the radius.

Unfortunately, we did not rear any adults from nymphs of this species; hence we cannot give a figure of the adult wing of this particular insect. But an examination of many Pentatomids shows that in the thickened portion of the fore wing the tracheæ follow essentially the same course as in the nymph figured here. There are also faint longitudinal veins in the membranous terminal portion of the wing which doubtless

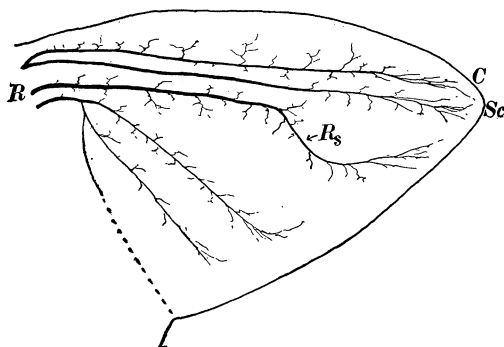


FIG. 22. — A Pentatomid, hind wing, nymph.

correspond with the tips and branches of the principal tracheæ. But at the base of the "membrane," as this terminal portion is designated by writers on the Hemiptera, a hinge line is formed, across which it is rarely possible to trace the tracheæ in dried specimens. The veins of the membrane appear to be connected by cross-veins parallel with this hinge line and close to it, and have but slight connection with the veins of the basal part of the wing except near the end of the anal furrow. We are not able, therefore, with the material at hand, to work out the homologies of the veins of the membrane, and must be content with pointing out at this time the more important features of the thickened portion of the wing.

In those Pentatomids in which we have been able to trace the courses of the tracheæ of the wings, the wing-veins are comparatively inconspicuous. We figure on this account one

of the Coriidae (*Hormostes reflexulus*) of which we have a specimen in which the tracheæ are distinctly visible within the well-developed veins (Fig. 23).

At the base of the wing the costa is remote from the costal edge of the wing, but approaches it near the middle of the

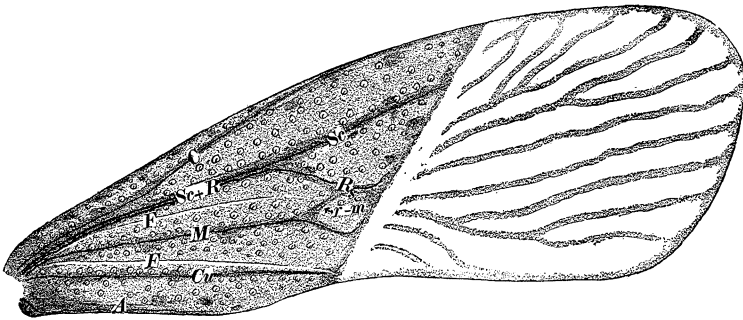


FIG. 23. — A Coreid, fore wing, adult.

thickened portion. The subcosta and radius coalesce to a point beyond the middle of this part of the wing, where the radial sector separates, making its characteristic curve. Vein  $R_1$  is wanting. Media, cubitus, and the first anal vein extend in nearly direct lines to the membrane.

The most important feature of the venation is the coalescence of subcosta and radius, a feature that occurs in many families of Hemiptera.

But the most important features to be observed are the positions of the furrows of the wing. Here the median furrow is in its typical position between radius and media. In the Pentatomids that we have studied it is more closely parallel with the radius and extends across the radial sector, showing that its position is not determined by the course of the veins. The anal furrow is in front of the cubitus instead of in its more usual position, behind this vein. In fact, in all of the Heteroptera that we have examined, when an anal furrow is distinctly developed it is in front of the cubitus.

Much remains to be done in tracing out the homologies of the wing-veins of the Hemiptera. But we feel that a good beginning has been made, one which will serve as a sure basis for future studies.



## VI. THE VENATION OF THE WINGS OF LEPIDOPTERA.

In the order Lepidoptera the primitive type of wing venation is well preserved in certain of the Jugatae. This is shown in *Sthenopis* (Fig. 24). In the species figured here, the deviations from our hypothetical type are few. In the fore wing, veins  $M_4$  and  $Cu_1$  coalesce for the greater part of their length, and one of the anal veins has been lost. In the hind wing, veins  $M_4$  and  $Cu_1$  anastomose, but separate near the margin of the wing.<sup>1</sup>

In the Frenatae we find the primitive type well preserved in the fore wings of the more generalized forms. The most striking departure from our hypothetical type is the fact that the

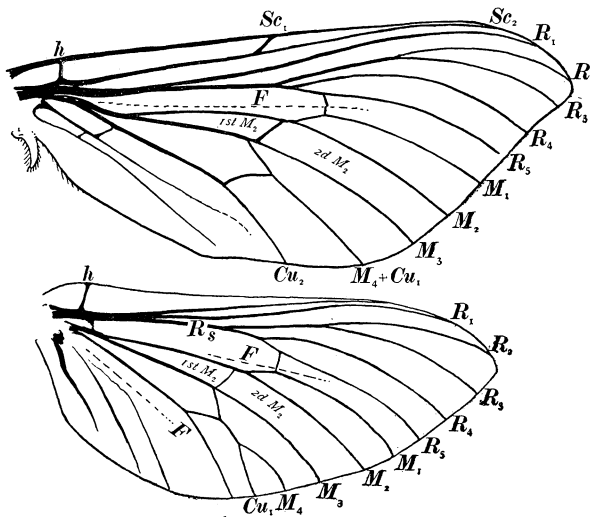


FIG. 24. — Wings of *Sthenopis*.

media is never more than three-branched;<sup>2</sup> and this is true also of the media of the hind wings. The wings of *Prionoxystus*

<sup>1</sup> This is not true of the genus as a whole; usually these veins coalesce in the hind wings as in the fore wings.

<sup>2</sup> With our present knowledge it is impossible to determine the way that vein  $M_4$  has disappeared in the Frenatae. We have seen no indication that it coalesces with vein  $Cu_1$  as in *Sthenopis*, for in all pupæ of this suborder that we have examined the medial trachea is only three-branched. We are obliged, therefore, to omit any further reference to this vein in the discussion of this order.

(Fig. 25) will serve to illustrate the type of venation characteristic of this suborder.

In the fore wing the branches of radius appear to present a complicated arrangement, but this is merely due to the anastomosis of veins  $R_3$  and  $R_4$ ; except for this the radial sector has preserved its primitive type. In this wing the bases of veins  $M_2$  and  $M_3$  have migrated towards the cubitus, so that cells 1st  $M_2$  and 2d  $M_2$  are not opposite each other (cell 1st  $M_2$  is the small triangular cell near the center of the wing).

In the hind wing a great reduction of the subcosto-radial

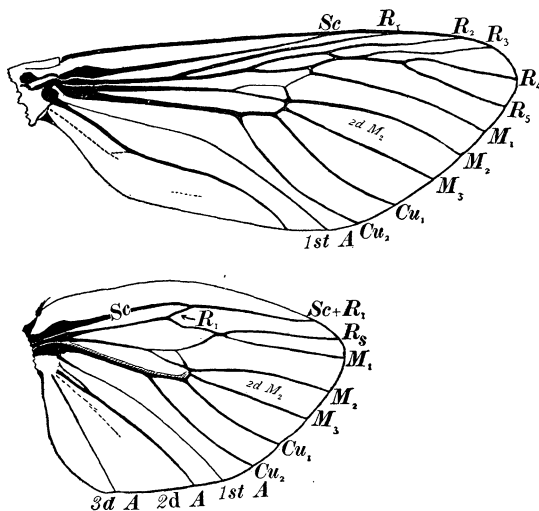


FIG. 25. — Wings of a *Prionoxystus*.

area of the wing has taken place. This has been brought about in two ways: first, veins  $Sc$  and  $R_1$  coalesce from the margin of the wing nearly to the base of  $R_1$ ;<sup>1</sup> and second, the radial sector is reduced to a single vein,  $R_s$ .

We have space to point out only one, the most important, of the ways in which this type is modified in the *Frenatæ*. It will be observed that the basal half of the wing, being traversed by the main stems of all of the veins, is stiffened to a great extent. Evidently, from what has taken place in the more specialized

<sup>1</sup>In pupæ of *Frenatæ* the subcostal trachea and the first branch of the radial trachea are distinct. This fact was first pointed out by Spuler.

families, there is more vein-material here than is necessary or perhaps desirable, for we find a very general tendency towards the atrophy of the base of the media.

An excellent record of what has taken place is preserved in the fore wing of the adult of *Anosia* (Fig. 26). Here the base of the media has disappeared, but there remain three little spurs projecting back into cell  $R+M$  (indicated by the arrows) which show the positions occupied by the three branches of the media when the base of this vein ceased to be of use. It should be

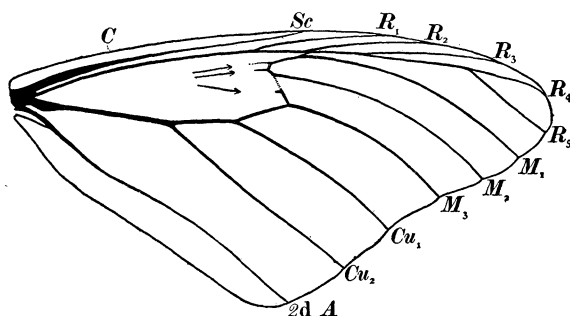


FIG. 26. — Fore wing of *Anosia*.

observed that in the pupa of this butterfly the medial trachea is well preserved throughout its entire length; the atrophy of the base of the media pertains only to the adult state.<sup>1</sup>

Correlated with the atrophy of the base of the media, there arises a necessity for a new source of air supply for the medial area of the distal half of the wing of the adult, and probably also for a better bracing of this part of the wing than would exist if no other changes were made. These are furnished by a more intimate connection of the branches of the media with the adjacent veins, vein  $M_1$  becoming more intimately connected with the radial sector, vein  $M_3$  with cubitus-one, and vein  $M_2$  with one or the other of these veins, differing in different families.

There result from the changes just pointed out striking modifications of the courses of the veins concerned. Note, for example, that the base of vein  $M_3$  in *Anosia* (Fig. 26) has

<sup>1</sup> Figures of the wings of pupæ of Lepidoptera are omitted, as several have been published by Spuler and others.

migrated away from the spur indicating its more primitive position, and that the medio-cubital cross-vein (*m-cu*) is no longer transverse, but appears to be a continuation of the main stem of the cubitus.

#### VII. THE VENATION OF THE WINGS OF TRICHOPTERA.

In the preceding pages much evidence has been given to show the importance of studying the tracheæ that precede the wing-veins, in order to determine with certainty the homologies of the latter. But in some of the orders of insects a remark-

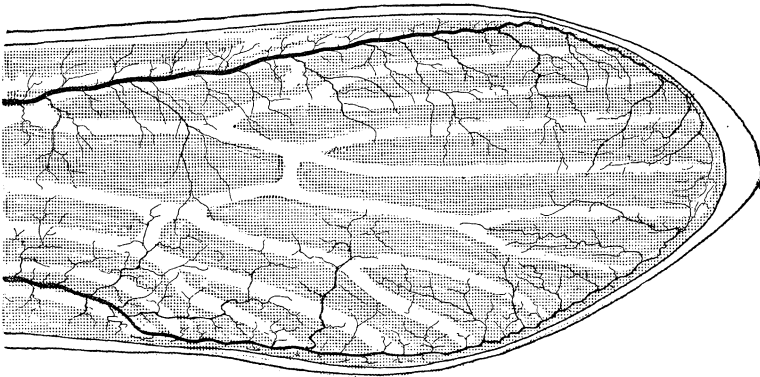


FIG. 27. — Wing of a pupa of a caddice fly.

able reduction of the wing tracheæ has taken place, which renders them useless for this purpose. This is true of the Trichoptera and Diptera, and also to a considerable extent of the Hymenoptera.

If the wing of a pupa of a caddice fly be examined at that stage when the forming wing-veins appear as pale bands, it will be seen that the tracheation of the wing bears but little relation to the wing-veins. Usually only two or three main tracheæ are present; and although these may coincide with forming veins, their branches bear no relation whatever to veins (Fig. 27).

Fortunately, in the case of the Trichoptera we do not need to study tracheæ in order to determine the homologies of the wing-veins; for here, in the more generalized members of the order, we find the primitive type of wing venation well preserved.

The fore wing of *Hydropsyche* (Fig. 28) with a slight modification would serve as a typical insect wing. Excepting the coalescence of anal veins at the tip, the number and arrangement of the longitudinal veins in this wing correspond exactly with our hypothetical type; and only those cross-veins are present that may be considered typical on account of the fre-

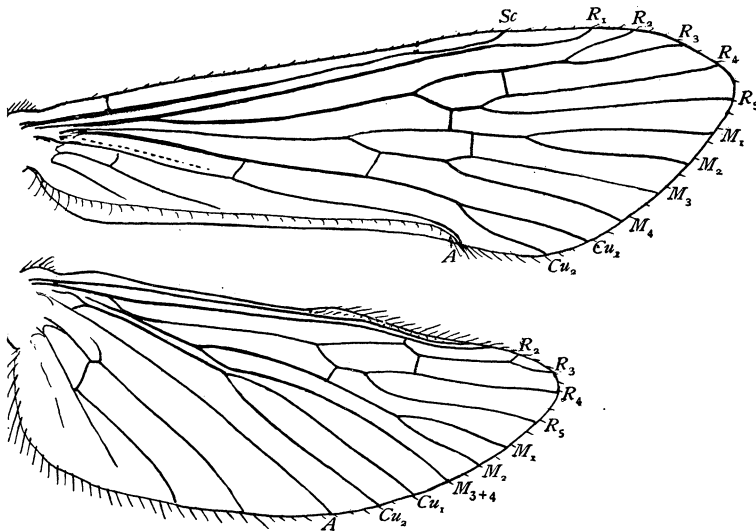


FIG. 28. — Wings of *Hydropsyche*.

quency with which they occur in the more generalized members of different orders.

In the hind wing the media is only three-branched and a tendency towards an increase in the number of anal veins is evident. This expansion of the anal area of the hind wings has been carried to a considerable extent in certain members of the order.

Lack of space prevents a discussion of the various ways in which the primitive type of wing venation is modified within this order. But such a discussion is hardly necessary, for it is not difficult to understand the venation of the wings of these insects.



## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER III (*continued*).

#### VIII. THE VENATION OF THE WINGS OF DIPTERA.

In the order Diptera, as in the Trichoptera, a great reduction of wing tracheæ has taken place. Owing to this fact we have not found that any light is thrown on the question of the homology of the wing-veins by a study of the tracheation of the wings of dipterous pupæ. We will, therefore, confine our attention in this place to a study of the wings of the adult.

In this order the tendency towards a cephalization of the flight function, which occurs in nearly all of the orders of

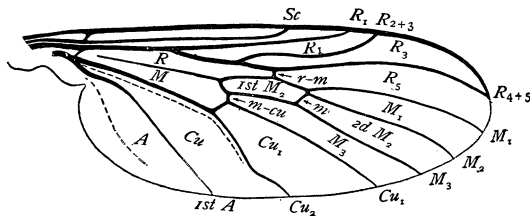


FIG. 29. — Wing of *Rhyphus*.

winged insects, reaches its maximum development, and has resulted in the complete suppression of the hind wings as organs of flight.

Notwithstanding this great modification of the organs of flight, the remaining pair of wings retain, in the more generalized members of the order, the primitive type of wing venation but slightly modified. So unimportant are the changes that the determination of the homologies of the wing-veins in these forms presents no difficulties.

If a wing of *Rhyphus* (Fig. 29) be compared with our hypothetical type (Fig. 5)<sup>1</sup>, it will be found to correspond very

<sup>1</sup> *American Naturalist*, April, 1898, No. 376, p. 251.

closely with it, the only differences being due to a slight reduction in the number of the veins ; the radial sector is reduced to a two-branched condition, the media is only three-branched, and only one of the anal veins is well preserved.

Although it is an easy matter to determine the homologies of the wing-veins in a generalized form like Rhyphus, it would be exceedingly difficult, if not impossible, to do this in the case of some of the more specialized forms if they alone were studied. But when a carefully selected series of forms is examined the difficulties vanish.

We wish now to call attention to such a series for the double purpose of demonstrating the homologies of the wing-veins in the more specialized forms and of showing the value in taxonomic work of the characters presented by the wings.

It should be borne in mind that the different parts of the wing may be modified more or less independently. Although the wing acts as a whole as an organ of flight, any change in the habit of flight is likely to result in a greater modification of some one part than of others. Thus we may find that in one line of descent a certain part is greatly modified and another part remains but slightly changed from the primitive type ; while in another line of descent the opposite may be the case. It is necessary, therefore, in discussing the changes that have taken place in the venation of the wings to treat the different veins separately. We will, however, refer to only a few of the more important of these changes, as a series of figures illustrating the homologies of the wing-veins of each of the families of this order has already been published by one of us.<sup>1</sup>

*The reduction of the radial sector.* — In a few genera of flies the radius retains the primitive, five-branched condition ; of these the genus *Protoplasa* of the Tipulidæ is a good example.<sup>2</sup> But usually the number of the branches of this vein is reduced by a coalescence of some of the branches of the radial sector. Thus in many families the radial sector is three-branched, in others it is only two-branched, and in the gall-

<sup>1</sup> Comstock, *Manual for the Study of Insects*, pp. 413-489.

<sup>2</sup> *Loc. cit.*, Fig. 504.



gnats (Cecidomyiidae) it is reduced to a simple, unbranched condition.<sup>1</sup>

As this variation in the number of the branches of this vein is due to a greater or less degree of coalescence among them, it is evident that here is a character of considerable taxonomic

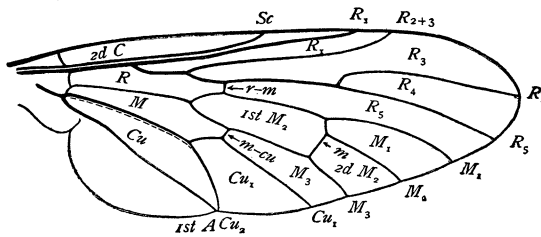


FIG. 30. — Wing of *Leptis*.

importance, serving as it does to indicate degrees of divergence from the primitive type.

Not only do we find differences in degree of reduction of this vein, but differences in the method of reduction are also shown. If the wing of *Leptis* (Fig. 30) and of *Dixa* (Fig. 31) be compared it will be seen that although in each the radial sector is only three-branched, the reduction has been brought about in a different way in the two genera. In *Leptis* veins

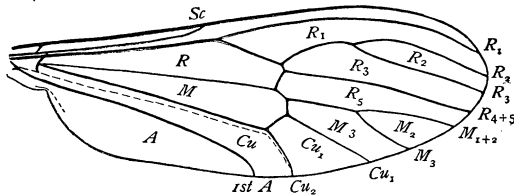


FIG. 31. — Wing of *Dixa*.

$R_2$  and  $R_3$  coalesce; while in *Dixa* it is veins  $R_4$  and  $R_5$  that have grown together. This is a difference in kind of specialization, which indicates that the two forms belong to different lines of descent. The common progenitor of these two genera had a four-branched radial sector; in some of the descendants of this primitive form one method of reduction has taken place, while in other descendants another method has been followed.

<sup>1</sup> *Loc. cit.*, Fig. 522.

That this differentiation took place comparatively early in the history of the order is shown by the fact that in all Nematocera that have a three-branched radial sector veins  $R_2$  and

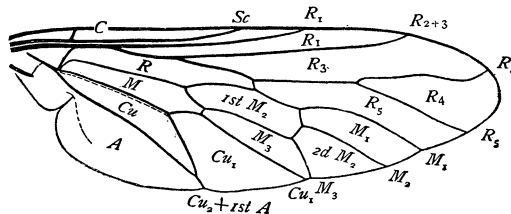


FIG. 32. — Wing of *Thereva*.

$R_3$  remain distinct; while in those Brachycera that have a three-branched radial sector veins  $R_4$  and  $R_5$  are separate.

*The coalescence of veins  $M_3$  and  $Cu_1$ .*—One of the most characteristic methods of specialization exhibited by the Dip-

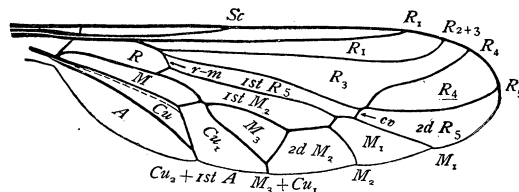


FIG. 33. — Wing of *Eulonchus*.

tera is the coalescence of veins from the margin of the wing towards the base. This method of coalescence may occur between any two adjacent veins, and sometimes occurs in two or three different regions of the same wing. The most strik-

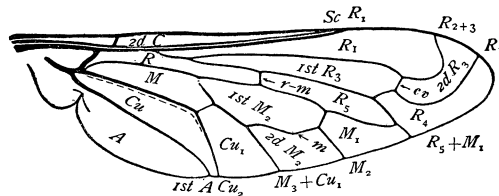
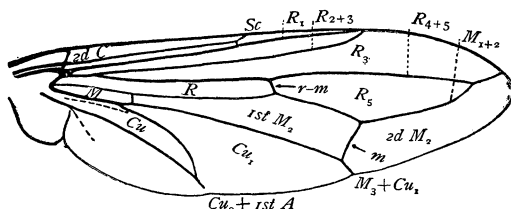


FIG. 34. — Wing of *Pantarbes*.

ing modifications in the courses of the wing-veins have been brought about in this way. Let us examine a series illustrating different degrees of coalescence of veins  $M_3$  and  $Cu_1$ .

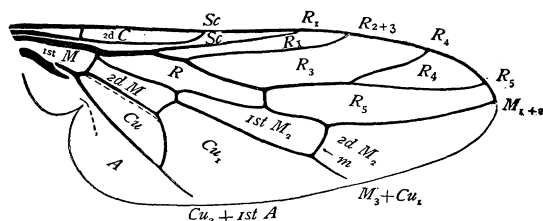
In *Rhyphus* (Fig. 29) these two veins retain their primitive position, extending nearly parallel and ending remote from

each other at the margin of the wing. In *Thereva* (Fig. 32) an approximation of the ends of these veins has taken place, which results in a narrowing of the outer end of cell  $M_3$ . In

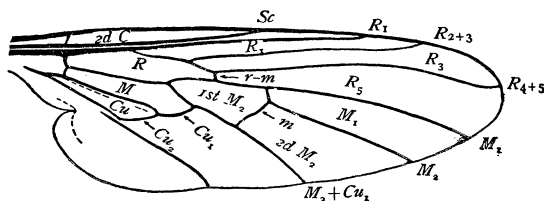
FIG. 35. — Wing of *Conops*.

*Eulonchus* (Fig. 33) the tips of the two veins coalesce, and cell  $M_3$  is thus closed. In *Pantarbes* (Fig. 34) the two veins coalesce for the greater part of their length, and cell  $M_3$  is completely obliterated.

*The coalescence of veins  $Cu_2$  and 1st A.*—The second branch

FIG. 36. — Wing of *Scenopinus*.

of the cubitus and the first anal vein may also coalesce in varying degrees. In *Rhyphus* (Fig. 29) these two veins retain their primitive position. In *Leptis* (Fig. 30) the tips are ap-

FIG. 37. — Wing of *Rhamphomyia*.

proximate. In *Thereva* (Fig. 32) the tips coalesce for a short distance. In *Conops* (Fig. 35) the coalescence is more striking. In *Scenopinus* (Fig. 36) it is carried still farther. While

in *Rhamphomyia* (Fig. 37) it has proceeded so far that vein  $Cu_2$  extends towards the base of the wing, and presents the appearance of a cross-vein.

It is not strange that the homology of the branches of the cubitus in forms like *Rhamphomyia* was not understood until the method of study used here was employed, but now there is no doubt regarding it.

The independent specialization of different parts of the wing can be seen by comparing members of the two series given above. Compare, for example, *Thereva* (Fig. 32) with *Pantarbes* (Fig. 34). If one were to consider only the degree of coalescence of veins  $Cu_2$  and *1st A*, *Thereva* would be considered the more highly specialized of the two genera, for in this genus these two veins coalesce for a considerable distance, while they are still distinct in *Pantarbes*. But if the degree of coalescence of veins  $M_3$  and  $Cu_1$  be considered the opposite conclusion would be reached, for in *Pantarbes* these veins coalesce for the greater part of their length so that cell  $M_3$  is completely obliterated, while in *Thereva* these veins are still distinct. No better evidence could be desired for showing the impossibility of arranging animals in a natural linear series. And it is not too much to hope that an exhaustive study along these lines will serve to determine the phylogeny of the families of this order.

ENTOMOLOGICAL LABORATORY,  
CORNELL UNIVERSITY, April, 1898.

## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER III (*Continued*).

#### IX. THE VENATION OF THE WINGS OF HYMENOPTERA.

The Hymenoptera belong to the series of orders in which the direction of specialization of the wings results in a reduction in the number of the wing-veins. This is true of the wing as a whole, the reduction taking place in the anal area of the wing as well as in the pre-anal area. We have found no representative of the order in which all of the veins have been preserved; and in the more specialized forms nearly all of the veins have disappeared.

A study of all of the families of the order shows that the most generalized of living forms, so far, at least, as concerns the structure of the wings, are to be found in the families Siricidæ and Tenthredinidæ. In these we find a close approximation in the number of wing-veins to the hypothetical type. But even here the courses of the branches of the forked veins have been greatly modified. These changes have been so great that the determination of the homologies of the wing-veins in this order was one of the most difficult problems of the kind that arose in the course of the study of the wings of insects.

This determination was made by the senior writer from an examination of the wings of adults before our present method of ontogenetic study was devised.<sup>1</sup> In the course of the present investigation we have endeavored to test the accuracy of his conclusions by a study of the tracheation of the wings of hymenopterous pupæ. We have found, however, that although the wings of the more generalized forms are abundantly supplied with tracheæ, the courses of these tracheæ have not been modified in the same way as have the courses of the veins with which they correspond. For this reason we are still forced to

<sup>1</sup> Comstock, *Manual for the Study of Insects*, pp. 603-607.



In the wings of these sawflies the anal furrow and the median furrow are both well marked, and are in the typical positions; that is, the anal furrow is immediately in front of the first anal vein, and the median furrow in front of the media. The furrows are represented by dotted lines in the figures.

In the anal area the three typical veins are preserved; but they coalesce to a considerable extent, both at the base and near the margin of the wing.

In the basal part of the pre-anal area the stems of the principal veins are as follows: the costa coincides with the costal margin of the wing (Fig. 38, *C*); the subcosta (*Sc*) is well preserved and is forked; back of the subcosta is a strong stem formed by the coalescence of the other three veins; the cubitus (*Cu*) soon separates from this stem, extending in a curve towards the anal furrow; while the radius and the media coalesce for about half their length. In order to make these veins more distinct in the figure we have marked the free portion of the media with cross lines.

When we pass from the consideration of the main stems to a study of the branches, we meet a much more complicated problem, a problem which could not have been solved by a study of Hymenoptera alone. But a knowledge of the methods of specialization of the wings of Diptera gives a key to an understanding of the wings of Hymenoptera.

In the preceding article of this series we pointed out that in many Diptera there is a marked tendency for veins to coalesce from the margin of the wing towards the base. In the Hymenoptera this tendency is much more marked and has been carried to a much greater extent, resulting in a very complicated arrangement of wing-veins, even in the most generalized members of the order.

If the reader will examine the series of figures illustrating the coalescence of veins *Cu*<sub>2</sub> and *1st A* in the Diptera,<sup>1</sup> he will find it easy to understand what has taken place in the Hymenoptera. In the Hymenoptera, however, both branches of the

in Macroxyela but in Macroxyela vein *Cu*<sub>2</sub> is lost. See Comstock, *Manual for the Study of Insects*, p. 606, for figures of the wings of these two genera.

<sup>1</sup> *American Naturalist*, vol. xxxii, No. 377, pp. 338, 339.

cubitus coalesce with the first anal vein; and this coalescence has proceeded so far that both branches cross the anal furrow and end in the anal vein remote from the margin of the wing.

It should be noted that vein  $Cu_2$  is rarely preserved in this order, even in the more generalized forms. We have found it

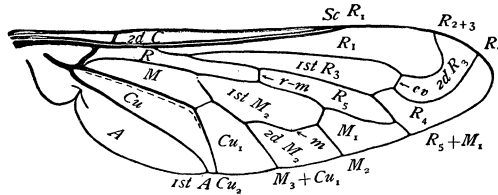


FIG. 40. — Wing of *Pantarbes*.

only in the genus *Pamphilius*. In *Macroxyela*<sup>1</sup> the position of the fork of the cubitus is indicated by a bend in this vein.

If the branches of the media be now examined, it will be seen that vein  $M_1$  (Fig. 38) extends longitudinally near the center of the distal part of the wing, its primitive course being modified slightly if at all. Vein  $M_2$  follows a course similar to the course of this vein in the dipterous genus *Pantarbes* (Fig. 40); so also does the medial cross-vein (Fig. 38,  $m$ ). A comparison of the position of cells  $M_1$ ,  $1st\ M_2$ , and  $2d\ M_2$  in these two genera (Figs. 39 and 40) is very instructive.

Returning to *Pamphilius* (Fig. 38), we see that vein  $M_3$  coalesces with the first anal vein, crossing the anal furrow near

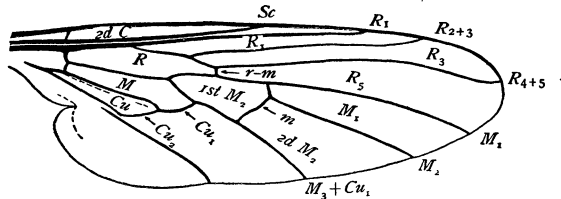


FIG. 41. — Wing of *Rhamphomyia*.

the margin of the wing. It is evident that the forces that are causing the branches of the cubitus to migrate along the first anal vein and towards the base of the wing are exerting a similar influence on this vein. It is also evident that vein  $M_4$  and  $Cu_1$

<sup>1</sup> Comstock, *loc. cit.*, Fig. 735.



coalesce at the tip, and that the migration of the united tips of these veins (marked  $Cu_1$  in the figure) towards the base of the wing has so modified the course of that part of vein  $M_4$  which is still free that this part of this vein extends towards the base of the wing. This change is very similar to the change in the course of vein  $Cu_2$  in the dipterous genus *Rhamphomyia* (Fig. 41).<sup>1</sup>

A curious result of this change in the direction of the course of vein  $M_4$  is that the cell  $M_4$  has been closed and pressed back to the center of the wing (Fig. 39,  $M_4$ ), and now lies in front of the free portion of vein  $M_4$  instead of behind it. A somewhat similar modification of cell  $M_3$  has been pointed out

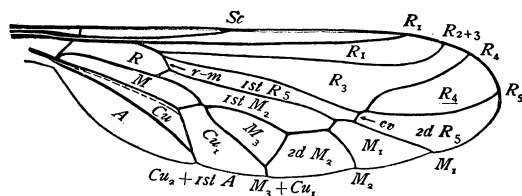


FIG. 42. — Wing of Eulonchus.

in the Diptera; we repeat the figure of the wing of *Eulonchus* for comparison (Fig. 42).

Let us now consider the courses of the branches of the radius. Here again we can gain help from a study of dipterous wings. Observe in *Pantarbes* (Fig. 40) the coalescence of the tips of veins  $R_5$  and  $M_1$ . In the Hymenoptera a similar coalescence of veins  $R_5$  and  $M_1$  has occurred; but it has proceeded much farther, so that the free portion of vein  $R_5$  in *Pamphilus* (Fig. 38,  $R_5$ ) is remote from the end of the wing and has the appearance of a cross-vein.

In the Hymenoptera vein  $R_5$  has been followed in its migration along vein  $M_1$  by vein  $R_4$ , which has now reached a stage in *Pamphilius* that is quite similar to that reached by vein  $R_5$  in *Pantarbes*. But like vein  $R_5$  it has the appearance of a

<sup>1</sup>At the time that the figures in Comstock's *Manual* were prepared it was believed that the media was typically three-branched. For that reason the vein which we now regard as vein  $\mathcal{M}_4$  was believed to be a cross-vein. The interpretation given above accords better with what we have since learned to be the typical form of the media.

cross-vein. In the fore wing of the honey-bee (Fig. 43) veins  $R_4$  and  $R_5$  still retain the appearance of branches of a forked longitudinal vein.

In *Pamphilius* vein  $R_1$  is curved away from the costal margin of the wing to make room for a stigma (Fig. 39, *S*), and vein  $R_3$  ends in the costal margin a short distance before the apex of the wing (Fig. 38). Vein  $R_2$  has been lost in this genus, but is well preserved in certain closely allied forms,<sup>1</sup> and is, therefore, represented in the figure.

While the tips of the branches of the radial sector have migrated away from the apex of the wing, the bases of these

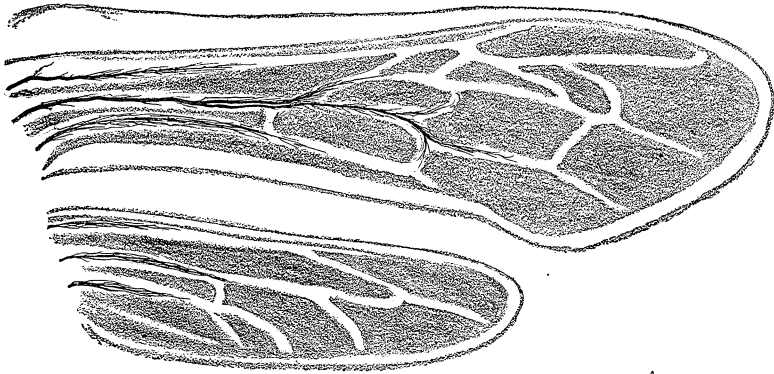


FIG. 43. — Wings of *Apis*, *young pupa*.

branches coalesce in the opposite direction; from these two causes results the transverse bracing of the radial area of the wing, which is a very characteristic feature of the venation of the wings in this order.

The details of these changes will be made clear by an examination of Figs. 44 and 45. The former represents the primitive mode of branching of the radius; the latter, the radial area of the typical hymenopterous wing (Fig. 38). In the hymenopterous type veins  $R_2 + 3$  and  $R_4 + 5$  of the primitive type coalesce so far that the branches of the sector arise from a common stem; and the tips of all of them have moved away from the apex of the wing, veins  $R_2$  and  $R_3$  following the costal margin of the wing; and veins  $R_4$  and  $R_5$  following

<sup>1</sup> See p. 414, footnote.

vein  $M_1$ . In the Hymenoptera a cross-vein has been developed between veins  $R_1$  and  $R_5$ . But this is not a peculiarity of this order; a similar cross-vein exists in many insects, and has been represented in our figures of the wings of a nymph of *Nemoura*.<sup>1</sup>

From the foregoing account it will be seen that even in the most generalized of living Hymenoptera there exists a highly

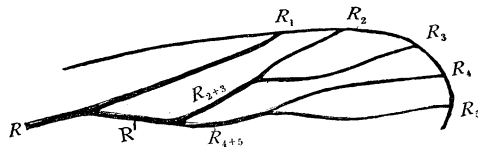


FIG. 44. — The typical radius.

modified wing venation. The indication of the details of the further modifications exhibited by the more specialized members of this order has already been done by one of us in another place. We will, therefore, merely refer to a single illustration.

When the fore wing of a honey-bee (Fig. 45) is examined it <sup>is</sup> found that, although this insect exhibits a wonderfully high development of instinctive powers, it retains a comparatively generalized wing venation. This wing, however, is much more modified than the fore wing of *Pamphilus*; and hence a comparison of the two is instructive.

In the honey-bee the subcosta is lost; so, too, is the second branch of the radius. Veins  $R_4$  and  $R_5$  retain a more general-

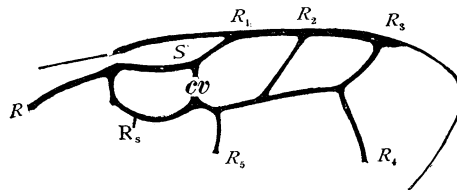


FIG. 45. — The radius in Hymenoptera.

ized condition than do these veins in the sawflies. The coalescence of the radius and the media extends farther than in *Pamphilus*, the base of the free portion of the media being carried farther from the base of the wing than the medio-cubital cross-vein (*m-cu*). This results in the base of the free

<sup>1</sup> *American Naturalist*, vol. xxxii, January, 1898, pp. 46, 47.

portion of the media ( $M$ ) being V-shaped. No trace of the second branch of the cubitus remains; and vein  $Cu_1$  appears as a short cross-vein, extending to the anal furrow near the middle of its course. But the most striking modification of all is exhibited by vein  $M_4$ ; the tip of this vein in its migration towards the base of the wing has passed over an arc of nearly  $180^\circ$ , so that now it extends from the point where it separates from vein  $M_3$  directly towards the base of the wing, and joins the medio-cubital cross-vein.

#### X. THE TRACHEATION OF THE WINGS OF HYMENOPTERA.

In our studies of the wings of the more generalized insects we found a close correlation between the venation and the tracheation of the wings. It can be accepted as a firmly established fact that the courses of the wing-veins of primitive insects were determined by the courses of preëxisting tracheæ. And one of the principal objects of the present investigation was to endeavor to settle certain questions regarding the homologies of wing-veins by a study of the tracheæ that precede these veins.

The importance of this method of study has been well shown by the results which we have obtained. But we also found that in the Trichoptera<sup>1</sup> there is little correlation between the venation and the tracheation of the wings, a remarkable reduction of the wing-tracheæ having taken place. A similar reduction of the tracheæ of the wings exists in most families of Diptera; and even when a large proportion of the tracheæ are retained, as in certain Asilids, they afford little aid in the determining of the homologies of the wing-veins. For this reason we omitted a discussion of the tracheation of the wings of Diptera. Again, in the Hymenoptera we find that the courses of the tracheæ cannot be depended upon for determining the homologies of the wing-veins. But here, in the more generalized members of the order, we find a very complete system of wing-tracheæ; and it is, therefore, incumbent on us either to point out the correspondence between the tracheæ

<sup>1</sup> *American Naturalist*, vol. xxxii, April, 1898, p. 256.

and the wing-veins, or to demonstrate that such a correspondence does not exist.

In the introductory article of this series,<sup>1</sup> in discussing the figures of the wings of a nymph of *Nemoura*, we called attention to the fact that the tracheæ in the wings of that insect extend in straight lines or in gentle curves, while in some cases the corresponding veins are much more angular; and we offered the following explanation of this phenomenon:

It is evident from this that in the perfecting of a wing as an organ of flight the position of a vein in the adult may become quite different from that of the corresponding trachea of the immature form. In other words, although there is no doubt that the courses of the principal wing-veins of

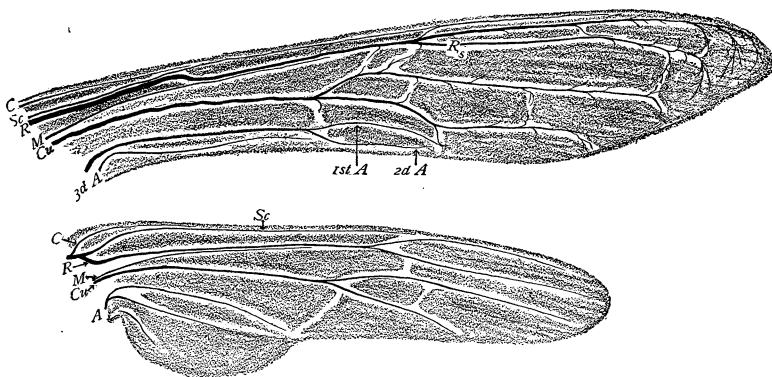


FIG. 46 — Wings of a pupa of *Tremex*.

primitive insects were determined by the position of the principal tracheæ of the wings, the wing-veins have been more or less modified to meet the needs of adult life; while at the same time the tracheæ of the immature wing, serving the purpose of respiration, and lying more or less free within the wing-sac, have not been forced to follow closely the changes in the cuticular thickenings of that sac.

In the Hymenoptera, as we have shown, the courses of the branches of the forked veins, in those forms where they have been preserved, have been so modified that these branches extend more or less transversely, making sharp angles with the main stems. It is not strange, therefore, that the tracheæ of the wings of the pupa lying free within the wing-sac, have not followed these changes.

<sup>1</sup> *American Naturalist*, vol. xxxii, January, 1898, p. 47.

Fig. 46 represents the wings of a pupa of *Tremex*; and Fig. 47, the fore wing of a pupa of *Apis*. In both cases the main tracheæ extend in nearly direct lines from the base of the wing to near its outer margin. This fact alone would indicate that the needs of respiration of the pupa, rather than the flight function of the adult wing, has been the important factor in determining the courses of these tracheæ.

A comparison of the fore wing of *Tremex* with that of *Apis* shows a remarkable difference in tracheation. In *Tremex* vein  $R_s$  is traversed by a branch of the radial trachea ( $R$ ); while in *Apis* the radial trachea is not branched, and the trachea traversing vein  $R_s$  arises from the cubital trachea ( $Cu$ ).

When this fact was first observed it was thought that the

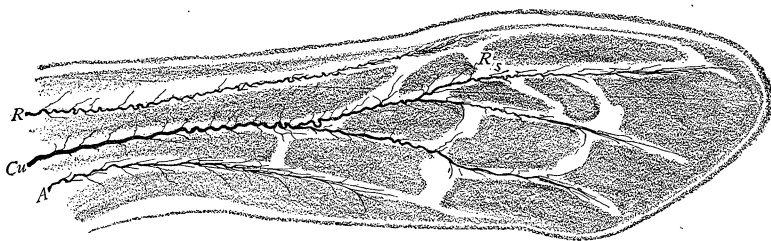


FIG. 47. — Fore wing of a pupa of *Apis*.

trachea of the radial sector in *Apis* had become transferred from the radial trachea to the cubital. We were not greatly surprised at this phenomenon, for a similar switching of tracheæ is common in those *Lepidoptera* in which the branches of the media become joined to the adjacent veins.

It was found, however, that this is not the explanation of the change. An examination of the wings of young pupæ of the honey-bee revealed the fact that in this insect the laying out of the wing venation precedes the tracheation of the wing. After the wing-veins reach that stage of development in which they appear as pale bands, the tracheæ grow out from the base 3/ of the wing into them. Fig. 48 represents the wings of a pupa taken at a stage which illustrates this pushing out of the tracheæ into the previously formed wing-veins.

It is obvious that tracheæ developed in this way will follow the paths offering the least resistance to their progress; and

that it is not to be expected that the tracheæ will preserve their primitive arrangement under these conditions. This brings us to the conclusion, already announced, that in determining the homologies of the wing-veins in the Hymenoptera we are forced to base our conclusions on a study of the veins themselves, and that a method of study which is of the highest importance in determining the homologies of the wing-veins in many other insects, is of little use here for this special purpose.

We have pointed out a striking difference in the tracheation

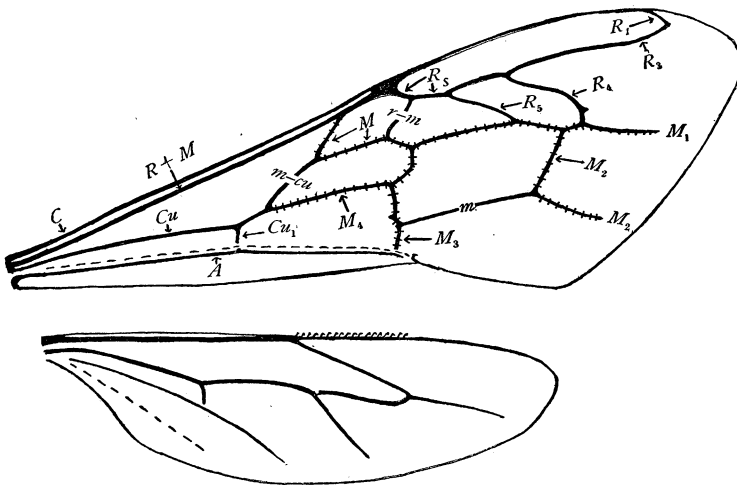


FIG. 48. — Wings of a young pupa of *Apis*.

of the fore wings of *Tremex* and of *Apis*. An equally striking difference may exist between the fore and hind wings of the same insect. Thus in the pupa of *Tremex* (Fig. 46) the main stem of the radial trachea traverses the subcosta in the fore wing; while in the hind wing it retains its primitive position. In more specialized members of the order, as in the Ichneumonflies, even less of the primitive arrangement of the tracheæ is preserved. But a further discussion of this phase of the question would not be profitable here.

#### XI. THE VENATION OF THE WINGS OF EMBIIDÆ.

The systematic position of the family Embiidæ is a question regarding which there is much difference of opinion. We do

not purpose to discuss this question here beyond pointing out that in the structure of the wings there is little in common between these insects and the Blattidæ and Mantidæ, with which they have been associated by Brauer,<sup>1</sup> or with the Termitidæ or Psocidæ, with which they are grouped by Sharp.<sup>2</sup> If we were forced to decide regarding the rank of this family from a study of the wings alone, we would be obliged to regard it as representing a separate line of development of ordinal value. But in this place we wish merely to offer a suggestion regarding the probable homologies of the wing-veins.

Fig. 49 represents the fore wing of *Oligotoma* and is based on a figure by Wood-Mason.<sup>3</sup> If this figure is correct, there is little difficulty in recognizing the principal veins. The only

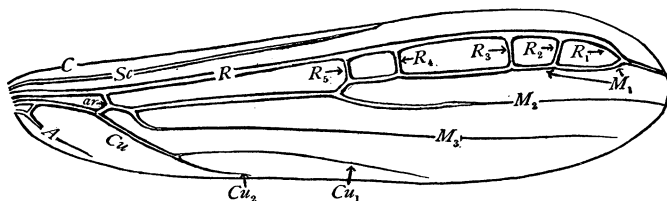


FIG. 49. — Wing of *Oligotoma*.

difficulty is presented by the four transverse veins on the distal half of the wing. After what we have seen in the wings of Diptera and of Hymenoptera, the most obvious interpretation of these is that they are branches of the radius, the tips of which coalesce with vein  $M_1$ . The result of this coalescence is that these veins have come to appear like cross-veins, as do veins  $R_4$  and  $R_5$  in the Hymenoptera. There is this striking difference, however: in the Hymenoptera only two branches of the radius bend back and unite with vein  $M_1$ ; in the Embiidæ all of the branches of the radius are modified in this way. And in the Embiidæ there is no indication of a similar backward bending of the branches of the cubitus.

ENTOMOLOGICAL LABORATORY,  
CORNELL UNIVERSITY, January, 1898.

<sup>1</sup> Friedrich Brauer, *Systematische-zoologische Studien*, p. 126.

<sup>2</sup> *The Cambridge Natural History*, vol. v, p. 342.

<sup>3</sup> *Proc. Zool. Soc. London*, 1883, p. 628.



## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER III (*Concluded*).

#### XII. THE VENATION OF THE WINGS OF COLEOPTERA.

The determination of the homology of the wing-veins of the Coleoptera is a difficult problem, owing to the greatly modified structure of the wings. Not only do the wings differ in structure from those of any other order of insects, but the two pairs of wings are modified in different ways. The fore wings, or elytra, have lost their flight-function, and have become thickened protective organs; while the hind wings are, in most cases, transversely folded, which has resulted in a great modification of the courses of the veins and in the formation of secondary vein-like thickenings of the wing.

So different is the structure of the elytra from that usually characteristic of wings that Meinert<sup>1</sup> was led to believe that they were not wings, but greatly enlarged paraptera of the mesothorax; and unfortunately this view was adopted by the senior writer in his *Manual for the Study of Insects*. We have, therefore, two questions before us: first, Are the elytra modified wings, or not? and, second, What are the homologies of the wing-veins?

The reasons in support of Meinert's view are the following: the difference in the structure of elytra from that of wings; the fact that in the Lepidoptera the paraptera of the mesothorax often bear a striking resemblance to elytra (this can be well seen by removing the scales from the paraptera, or patagia, as they are termed, of a sphinx moth); and the fact that in many Coleoptera (*e.g.*, *Dytiscus*) what appear to be rudiments of the fore wings exist beneath the elytra.

The argument based on the thickened structure of the elytra loses its force when we consider the more or less elytra-like

<sup>1</sup> Meinert, F. *Entomologisk Tidskrift*, p. 168. 1880.

wings of many other insects (Heteroptera, certain Blattidæ, *et al.*); and it probably would not have been seriously urged but for the presence of the so-called rudimentary wings beneath the elytra of certain beetles.

When, however, the supposed rudimentary wings are examined, they are found to correspond in structure and position to the alulæ of the wings of other insects. The most conclusive evidence of this correspondence is the fact that they are margined by the cord-like structure which has been termed the

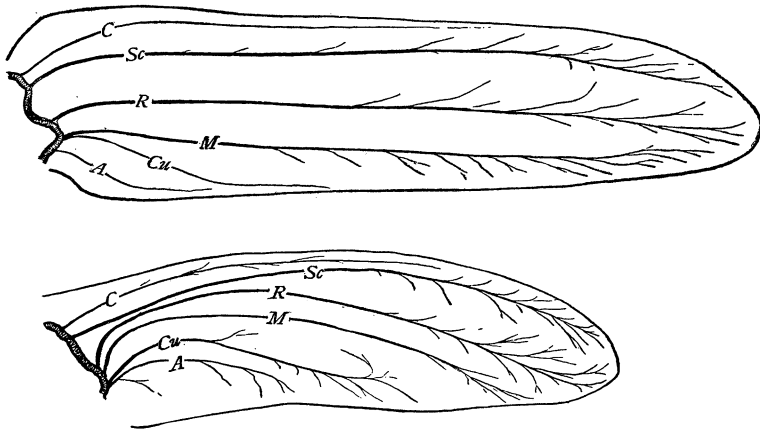


FIG. 50. — The tracheation of the wings of a cerambycid pupa.

spring-vein. This arises from the caudal border of the scutellum, and is a distinctive characteristic of this portion of the wing. The presence of these membranes beneath the elytra, therefore, merely indicates that if the elytra are modified wings they do not correspond to entire wings but to wings minus the alulæ.

When the elytra of a pupa of a beetle are examined, they are found to be traversed by several, usually five or six, longitudinal tracheæ. Although these tracheæ may give rise to a greater or less number of smaller tracheæ, there is nothing in the branching of them, in any of the forms that have as yet fallen under our observation, that corresponds with the branching of the tracheæ in our hypothetical type. But as this is almost as true of the hind wings, it has little bearing on the question of

the homology of the elytra. We are forced to conclude that in this order the wings are so modified that the typical branching of the veins is lost. We have examined, however, a comparatively small series of coleopterous pupæ; and it is quite possible that generalized forms may yet be found in which the typical branching of the veins is preserved.

We refer to the veins instead of to the tracheæ in this connection, as some observations that we have made indicate that in the Coleoptera as in the Hymenoptera the venation of the

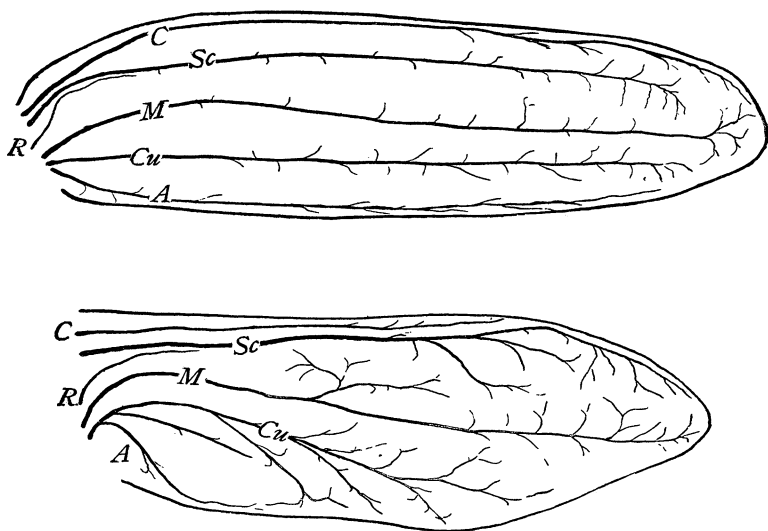


FIG. 51. — The tracheation of the wings of a cerambycid pupa.

wings precede their tracheation, and that the courses of the main tracheæ are determined by the courses of the preëxisting veins.

Returning to the question of the homology of the elytra, the most conclusive evidence that we have found is the fact that a very close correspondence exists between the tracheation of the elytra and that of the hind wings. And what is especially striking is that similar modifications occur in the two pairs of organs.

The accompanying figures of the elytra and wings of two cerambycid pupæ illustrate this point. And the lettering of

these figures will serve to show our conclusions regarding the homologies of the tracheæ.

In the species represented by Fig. 50, the radial trachea is the most prominent one in both elytra and hind wings. On the other hand, in the species represented by Fig. 51, the radial trachea is reduced in both elytra and hind wings to a mere rudiment. If the elytra and hind wings were not homodynamous organs, it is not probable that the modifications of the two would be so closely correlated. We conclude, therefore, that the elytra are modified wings.

In comparing the tracheation of the elytra with that of the hind wings, the most striking difference observed is the greater

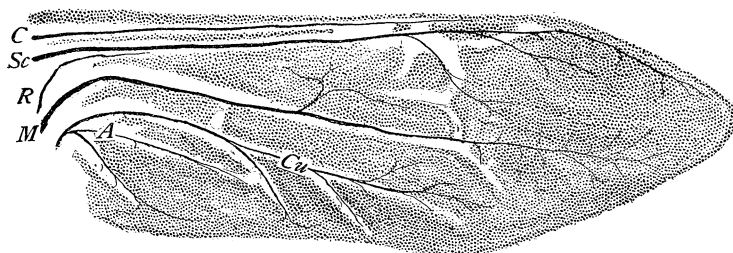


FIG. 52. — Hind wing of a pupa of a beetle.

reduction of the anal area of the former. This is doubtless due to the fact that the meeting of the elytra when at rest in a straight line along the middle of the back does not admit of an expanded anal area.

The extent of the correspondence between the venation and the tracheation of the hind wing of a full-grown pupa is shown by Fig. 52. The principal tracheæ are within the veins, but the branches of these tracheæ extend irregularly through the wing. In the region where the wing is to be folded the secondary vein-like thickenings are only partially supplied with tracheæ.

Although the veins of elytra of adult beetles appear in many cases as well-marked ridges, when elytra of pupæ are prepared, as we prepare wings for this purpose, and examined by transmitted light, we do not find any difference in color between the forming veins and the spaces between them.

With this we conclude our discussion of the venation of the series of forms illustrating the specialization of wings by reduction. The sequence in which the forms have been discussed has been determined merely by convenience, except that we believe that the Plecoptera, which were treated first, resemble the primitive winged insect in the tracheation of their wings more closely than do the members of any other order as a whole. In the next chapter we will give some illustrations of the specialization of wings by addition.

ENTOMOLOGICAL LABORATORY,  
CORNELL UNIVERSITY, May, 1898.



## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER IV.

#### *The Specialization of Wings by Addition.*

##### I. THE DEVELOPMENT OF ACCESSORY VEINS.

THE more important of the generalizations reached in the course of the present investigation are two in number ; first, the recognition of certain features of the venation of the wings of insects, which occur in the more generalized forms of a large proportion of the orders of this class, has enabled us to present a hypothetical type to which the wings of all orders may be referred ;<sup>1</sup> second, if we leave out of consideration the anal area, that portion of the wing traversed by the anal veins, we will find that in nearly every case each order of insects is characterized by either a reduction or a multiplication of the wing-veins ; in certain orders the tendency is in one direction, while in others it is in the opposite ; but either of these tendencies may be correlated with a similar tendency in the anal area or with the opposite one.

In the preceding chapter we pointed out the various ways in which the number of the wing-veins in the preanal area is reduced. In nearly every case we found the reduction of the preanal area accompanied by a similar tendency in the anal area, or, if a reduction had not taken place, there was no increase in the number of veins of this area, the tendency being towards the production of a few-veined wing. The Trichoptera, however, form an exception to this rule.

We have now to consider several types of wings, in each of which there is taking place an increase in the number of veins of the preanal area, the tendency being towards the formation of a many-veined wing. In speaking of an increase in the number of veins, reference is made only to a multiplication

<sup>1</sup> *American Naturalist*, vol. xxxii (February, 1898), pp. 81-89.

of the branches of the principal veins. In no case is there an increase in the number of principal veins. And this increase in the number of branches may be confined to one or two of the principal veins, while the number of the branches of some of the other veins may be reduced, the expanding of some parts of the preanal area resulting in a crowding of other parts. In some cases we will find that the multiplication of wing-veins extends to the anal area also ; in others we will find the anal area greatly reduced. But even in those cases where the anal area is reduced, the total result has been the production of a many-veined wing.

In the many-veined wings both the longitudinal veins and the cross-veins are increased in number. In most cases where there are many cross-veins it is impracticable to distinguish from others those particular cross-veins to which we applied special names in describing the few-veined wings.<sup>1</sup> But in the case of the longitudinal veins it is necessary to distinguish the primitive veins, that is, those of our hypothetical type, from the veins that have been developed in addition to these. For if this is not done it will be impossible to point out the changes that have taken place in the course of the development of each of the various types of many-veined wings. We therefore apply the term accessory veins to these secondarily developed longitudinal veins, and retain the same nomenclature for the primitive veins that we used in describing the few-veined wings.

Accessory veins may be borne by any of the primitive longitudinal veins ; and they may arise from either of the two sides of such a vein. In most cases it is unnecessary to designate the individual accessory veins, as, usually, it will be sufficient for descriptive purposes to indicate the number of these veins that have been developed upon a particular longitudinal vein. In fact, in certain cases more than this could not well be done owing to the irregularity of the veins. On the other hand, in many cases the accessory veins borne by a single primitive vein present a high degree of regularity, and it is evident that they have been developed in a regular sequence. Under these

<sup>1</sup> *American Naturalist*, vol. xxxii (April, 1898), pp. 233, 234.



circumstances it is practicable to designate them individually; and we have devised the following method for this purpose.

The accessory veins arising from one side of a single primitive vein are considered as a single set, and to each set of veins a distinct set of numbers is applied, beginning with the oldest (*i.e.*, the first-developed) member of the set.

By this method homologous veins, when a homology exists, will bear the same number. But it should be remembered that as accessory veins have arisen independently in many different groups of insects, it often happens that accessory veins similar in position, and bearing the same number in our system, are merely analogous and not homologous.

In order to apply this system it is necessary to know, in the case of each group of insects studied, the sequence in which the members of the particular set of veins under consideration have been developed. For additions to such a set of veins may be made to the distal end of the series, or to the proximal end, or may be interpolated at some distance from either end.

Frequently an examination of the wing of an adult insect is sufficient to determine this sequence. But the determination can be made in a much more satisfactory manner by a study of the tracheation of the wings of the nymph or pupa. For in the many-veined insects the longitudinal veins, both primitive and accessory, are developed about tracheæ; and it is much easier to determine the homologies of the tracheæ of an immature wing than it is to determine the homologies of the wing-veins of the adult. And, too, in this way we are able to eliminate the cross-veins which are not preceded by tracheæ in the forms used for illustration here. We will, therefore, use for this purpose the wings of immature insects.

*Accessory veins added distally.* — If the radial tracheæ of the pupa of *Chauliodes* (Fig. 53) and of the pupa of *Corydalus cornuta* (Fig. 54) be examined, it will be seen that both differ from our hypothetical type in the presence of a greater number of branches of the radial sector. And a comparison of the two figures shows that the increase in the case of *Corydalus* has been greater than in the case of *Chauliodes*. Farther, the presence of fine twigs at the tip of the trachea  $R_s$  indicates the

method of increase, which is doubtless as follows: the branches have been added one after another to the tip of trachea  $R_2$ , there being a migration of the base of each accessory trachea towards the base of the wing, thus making room for the addi-

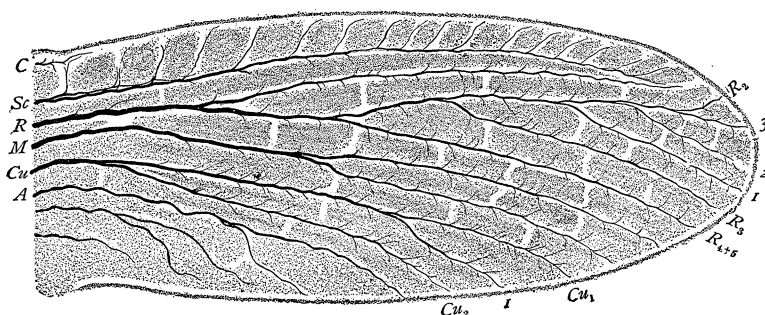


FIG. 53. — Wing of a pupa of Chauliodes.

tion of new branches. In this case the first accessory vein is the proximal one.

In *Sialis* (Fig. 55) the accessory veins have been developed in a similar way, but they are on vein  $R_3$  and on the cephalic side of this vein. Here, too, the first accessory vein is the proximal one. But it should be noted that the numbers of the veins increase in the opposite direction from what they do when the

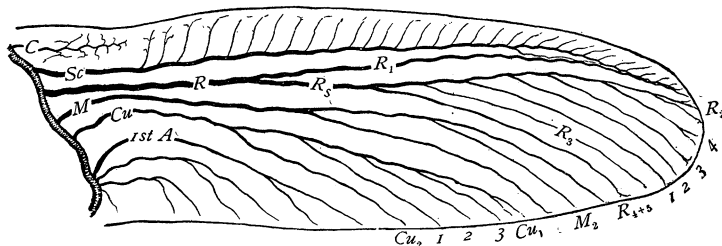


FIG. 54. — Wing of a pupa of Corydalis.

accessory veins are added distally on the caudal side of a primitive vein, as in the radial sector of Chauliodes and Corydalis.

*Accessory veins added proximally.* — A good illustration of the adding of accessory veins to the proximal end of a series is afforded by the accessories of vein  $Cu_1$  in the Blattidæ. Fig. 56 represents the hind wing of a nymph of a cockroach. An

examination of the set of accessory veins borne by vein  $Cu_1$  shows that the distal members of the series are well developed, and that the growth of additional veins is taking place in the disk of the wing at the proximal end of the series. In this case the first accessory vein is the distal one.

*Accessory veins interpolated.* — In the wing of the cockroach

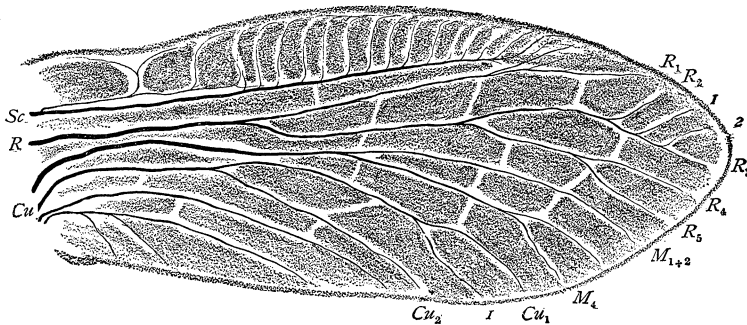


FIG. 55.— Wing of a pupa of *Sialis*.

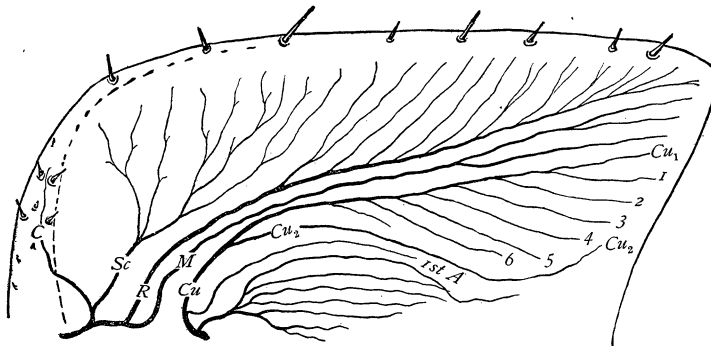


FIG. 56.— ~~Hind~~ wing of a nymph of a cockroach.

represented by Fig. 56 there are many accessory veins borne on the cephalic side of radius. From the presence of the fine twigs near the apex of the wing, it is evident that accessory veins are being added distally. It is also evident that the number of veins is being increased by the splitting of certain of the older veins, *i.e.*, by interpolation. In cases of this kind it is impracticable to number the members of a series of accessory veins.

## II. THE SUPPRESSION OF THE DICHOTOMOUS BRANCHING OF VEINS.

In the more highly specialized of the many-veined insect wings there exists a type of branching which is very different from that of our hypothetical primitive type. An examination of Fig. 57, which represents this type, will show that in every case the forked veins are branched dichotomously, while in the many-veined wings the more characteristic type of branching results in the formation of pectinate veins; this pectinate type of branching is well shown by the radial sector of *Corydalis* (Fig. 54).

The prevalence of the pectinate type of branching in the many-veined wings has been, doubtless, the greatest obstacle

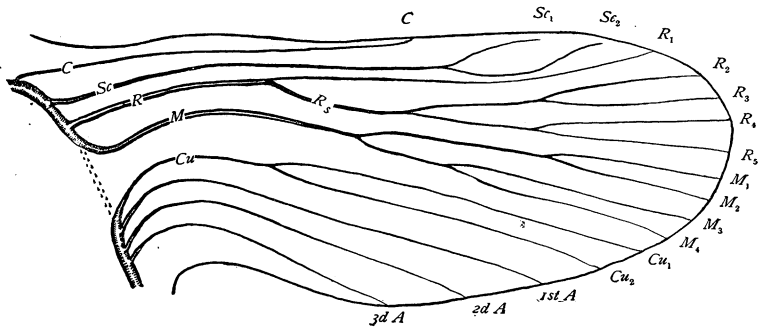


FIG. 57. — Hypothetical type.

to a recognition of the homologies of the branches of the forked veins in such wings. Our hypothetical type was first worked out by a study of the few-veined wings; but it was a long time after that was accomplished before we saw that the pectinate type of branching had been derived from the same type. The most potent factor in reaching this conclusion was the fact that in some of the many-veined insects the dichotomous type of branching has been preserved. Good illustrations of this can be seen in the neuropterous genus *Sialis* (Fig. 55), while equally good examples of the pectinate type are presented by the closely allied genera *Chauliodes* and *Corydalis* (Figs. 53, 54).

The changes that take place in the development of the pectinate type of venation from the dichotomous type are of two

kinds: first, the development of accessory veins; second, the modification of the primitive veins so that they are no longer dichotomously branched. The former has been discussed above; we will now briefly refer to the latter. For this purpose we will give a series of diagrams illustrating several types of branching of the radial sector.

Fig. 58*a* represents the typical or dichotomously branched radial sector. Fig. 58*b* represents a typical radial sector with the addition of some accessory veins on the caudal side of vein  $R_2$ . Such a radial sector occurs in the fore wing of *Ithone*.<sup>1</sup> In this case the radial sector is nearly pectinate, but not quite so, owing to the forked condition of vein  $R_{4+5}$ . In *Chauliodes* (Figs. 53, 58*c*) veins  $R_4$  and  $R_5$  coalesce to the margin of the wing; and in this way the pectinate type is attained. In *Hemerobius* (Figs. 58*d*, 59) the pectinate type has been attained by fission instead of coalescence. Here veins  $R_4$  and  $R_5$  have split apart till vein  $R_5$  arises from the main stem of radius.

When many cross-veins are present, the dichotomy of the branching of the sector may be suppressed in still another way, by the transference of the base of vein  $R_4$  to

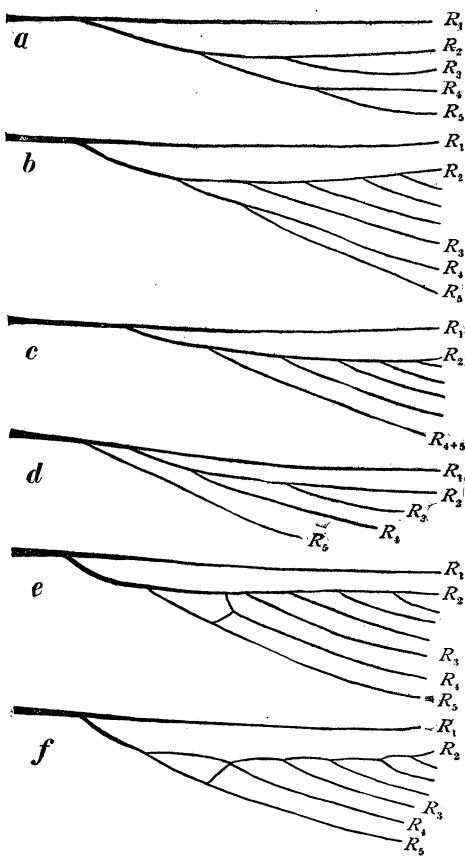


FIG. 58. — Diagrams of several types of radius.

<sup>1</sup> Brongniart. *Rech. sur l'Hist. d. Insectes Fossiles*, Pl. I, Fig. 10.

vein  $R_{2+3}$ . All stages of this switching of vein  $R_4$  occur in the Myrmeleonidæ; but two examples will suffice to illustrate it. In Myrmeleon (Fig. 58e) the base of vein  $R_4$  appears to be forked; one arm of the fork arising from vein  $R_5$ , the other from vein  $R_{2+3}$ . The former is the true base of vein  $R_4$ ; the latter is a cross-vein which is assuming the function of a base of this vein. In the hind wing of *Ptynx appendiculatus* (Fig. 58f) the switching has been completed, vein  $R_4$  arising from vein  $R_{2+3}$ .

In the foregoing illustrations comparisons of allied insects have been made in order to determine the ways in which the wings are being modified; frequently a comparative study of the fore and hind wings of a single insect is equally suggest-

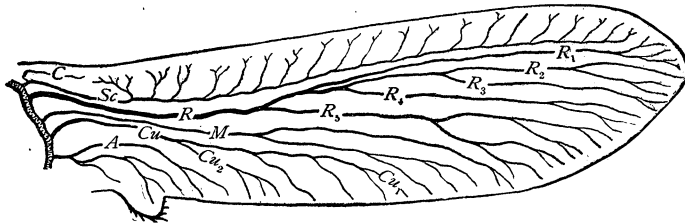


FIG. 59. — Wing of a pupa of Hemerobius.

ive, for it often happens that the two pairs of wings exhibit different degrees of the same kind of modification, and thus the course of the change is indicated.

A study of the causes of the changes which we are describing is beyond our present purpose, which is merely to determine the homologies of the wing-veins. But we can gain a hint of the probable reason for the development of the pectinate type of veins without entering very deeply into questions of the mechanics of flight.

It is obvious that many styles of flight exist among insects, and that for the different styles of flight different kinds of wings are required. In *Corydalis* (Fig. 54) the wing is stiffened, along a line parallel with the costal margin of the wing, by the subcosta, the main stem of the radius, and veins  $R_1$  and  $R_2$ . Back of this line there is a broad, flexible area, which bends up during the downward stroke of the wing, forming an inclined plane, the pressure of which against the air forces the

insect ahead. The flexibility of this area of the wing is increased by those changes which result in the formation of the pectinate type of branching.

The extreme of the pectinate type of branching exists in the neuropterous genus *Polystœchotes*, in which the area traversed by the parallel veins is very broad.





## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER IV (*continued*).

#### *The Specialization of Wings by Addition.*

#### III. THE VENATION OF THE WINGS OF ODONATA.

THE wings of dragon flies have furnished the best of systematic characters since the days of Linnæus. The many peculiarities of venation have been slowly worked out and expressed in a formidable system of terms, most of which designate parts bearing other names in other orders. Indeed, this is not strange ;

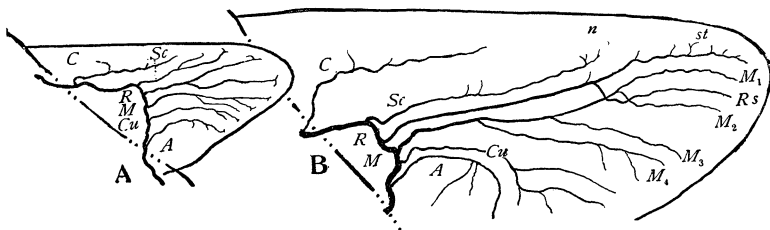


FIG. 60.—Wings of nymphs of *Gomphus desertus*, early stages.

for, from the study of the adult wings alone, the discovery of the real homologies would be well-nigh impossible.

The richly veined wing of a dragon fly, at first sight, shows little in common with our hypothetical type. And even when the tracheation of the wing of an old nymph is studied, there are found some striking discrepancies. But in the budding wing of a young nymph we find an arrangement of the tracheæ which is almost that of the typical wing.

Fig. 60 represents the tracheation of two nymphs of *Gomphus desertus*. The wing figured at A was only 1 mm. in length. Here is a costa with some anterior twigs, a subcosta with a terminal fork, a radius with its sector unbranched, a three-branched media, a cubitus which is two-branched in the usual

way, and a single anal vein with three branches, which may represent the three anal veins, fused at the base.

At *B* (Fig. 60) is represented the tracheation of a somewhat older wing, one measuring 3 mm. in length. Here the radial sector has shifted its position and lies across the end of the media, the terminal portion of it lying between  $M_1$  and  $M_2$ . The media is now four-branched. The costal and anal tracheæ

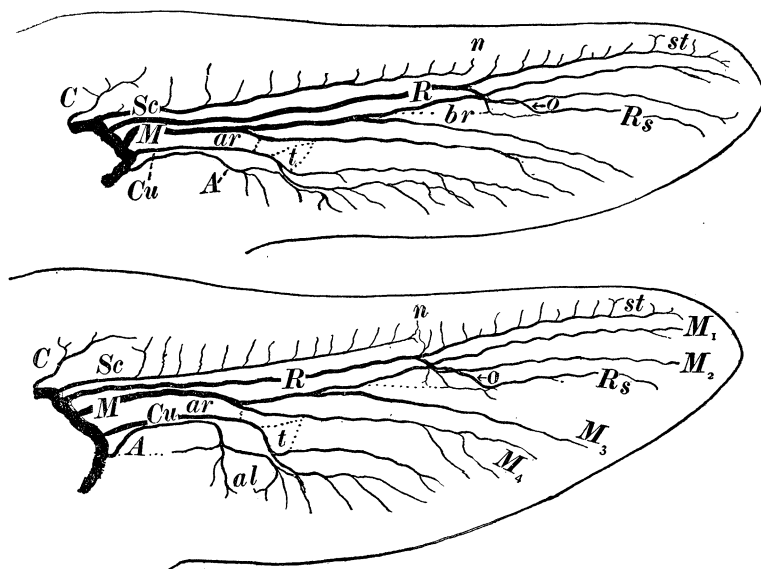


FIG. 61. — Fore and hind wings of a nearly grown nymph of *Cordulegaster diastatops*, showing tracheæ. *n*, nodus; *st*, stigma; *o*, oblique vein; *br*, bridge; *ar*, arculus; *t*, triangle; *al*, anal loop. The permanent venation which shows distinctly at this stage is omitted, except where indicated by dotted lines at the bridge, arculus, and triangle.

are outrun by the others in the occupation of the new territory formed by the growth of the wing, and remain relatively short.

In the wings of a grown nymph (Fig. 61) is seen the culmination of these tendencies. The radial sector has completed its migration and lies in its final position, the terminal portion traversing the area between  $M_2$  and  $M_3$ . The costa is greatly reduced or, rather, outstripped by its competitors; the same is true in a less degree of the subcosta and the anal vein. At this stage the veins, which are not represented in the figure, appear as pale, brownish thickenings; surrounding all of the

principal tracheæ, and also surrounding the anastomosing tracheoles, which tend to group themselves in the positions of the cross-veins.

The most anomalous thing seen here is the position of the radial sector, a character which is quite distinctive of this order. In the adult wing (Fig. 62) this sector appears to be a branch of the media, and it has always been so interpreted. The only indication of its connection with the radius is the persistent obliquity of an apparent cross-vein between veins  $M_2$  and  $R_s$ , just beyond the nodus.

The crossing of these tracheæ (Fig. 61) was first figured

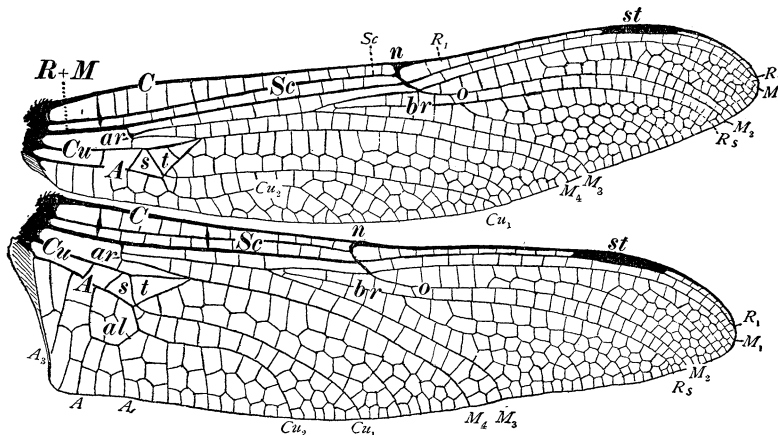


FIG. 62. — Adult wings of *Cordulegaster sayi*, lettered as in Fig. 61.

(incidentally) by Roster;<sup>1</sup> later it was described and discussed by Brauer and Redtenbacher;<sup>2</sup> and it was again figured and described by Brogniart.<sup>3</sup> But the effect of this crossing upon the homologies of the veins seems to have been overlooked. The apparent cross-vein is, in fact, a part of the radial sector; the longitudinal trunk connecting the sector with the media is not homologous with any of the principal veins, but is a secondary structure, developed for mechanical advantage, and the radial sector itself should be so termed, notwithstanding it appears to be a branch of the media and is far removed from

<sup>1</sup> Roster, D. A. *Bull. Soc. Ent. Ital.*, vol. xvii (1885), Pl. IV.

<sup>2</sup> Brauer u. Redtenbacher. *Zool. Anz.*, Bd. xi (1888), pp. 443–447.

<sup>3</sup> Brogniart. *Recherches sur les Insectes Fossiles* (1894), pp. 204–208, Pl. VIII.

its usual position. It will be convenient to designate that part of the radial sector which appears as a cross-vein behind vein  $M_2$  as the *oblique vein* (Fig. 62, *o*); and the secondary longitudinal trunk as the *bridge* (Fig. 62, *br*).

In the adult wing the bridge exhibits no evidence of an origin different from that of the radial sector, with which it is strictly continuous. But a study of the tracheation of the

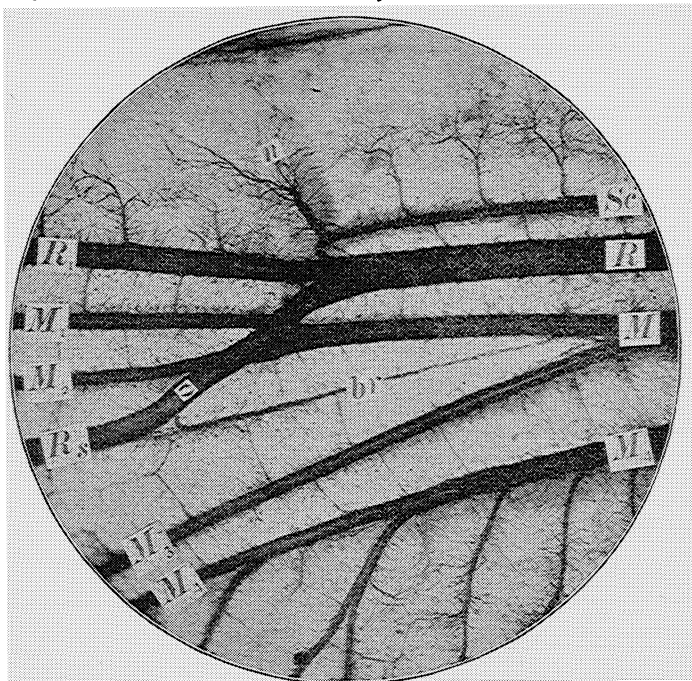


FIG. 63. — The region of the nodus in *Anax junius*, showing the crossing of the radial sector and the origin of the trachea which precedes the bridge. *o*, oblique vein; *br*, the bridge.

wings of nymphs reveals the secondary nature of the origin of the bridge. Fig. 63 is a reproduction of a photograph of a portion of a wing of a nymph of *Anax junius*, showing the crossing of the radial sector, and the origin of the trachea which precedes the bridge. The latter is a small twig which arises from the distal end of that portion of the radial sector which becomes the oblique vein, and extends towards the base of the wing in a direct line to the media. This method of formation of the bridge is characteristic of the *Æschnidæ*.

In most Libellulidæ a trachea, or a bunch of tracheoles, descends from near the base of the radial sector and forks at the level of the bridge, one branch going to the distal end of the oblique vein, the other going in a diametrically opposite direction to the media (Fig. 64).

The illustrations just given exhibit the structure of these parts in nymphs of the suborder Anisoptera. In the suborder Zygoptera (Calopterygidæ and Agrionidæ) there exists a strik-

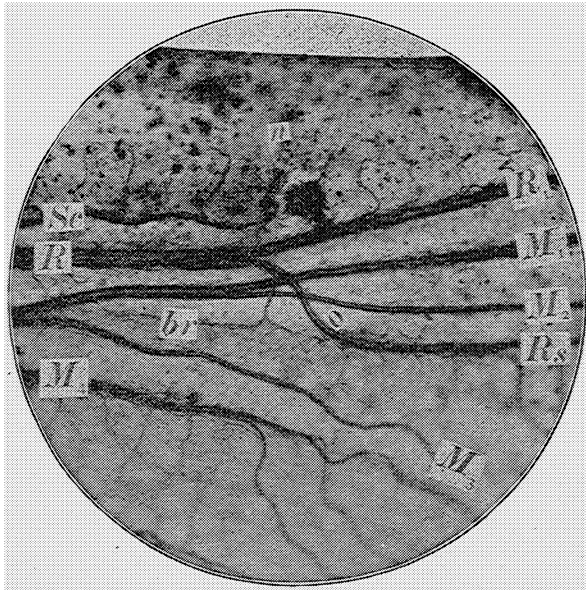


FIG. 64. — The region of the nodus in *Libellula pulchella*. *o*, oblique vein; *br*, the bridge.

ing difference. If we compare adult wings of the two suborders, there can be no question as to the identity of vein  $R_s$ , or as to its homology in the two groups. But in the suborder Zygoptera, so far as known to us, the trachea  $R_s$  is a branch of the medial trachea. The base of  $R_s$ , however, forms an oblique vein, and a bridge is developed secondarily, as in the Anisoptera. It is probable that there has been a switching of the base of the trachea  $R_s$  from trachea  $R$  to trachea  $M$ . One has only to examine a well-mounted wing of any dragon-fly nymph to see in the universal anastomoses of tracheoles communications already set up between principal tracheæ, any one of which

might be enlarged, should necessity arise for the entrance of air from a new quarter. Following this, the atrophy of the old connection would complete the switching; which, we believe, is what has happened in the Zygoptera. It follows from this that, so far as this portion of the wing is concerned, the Zygoptera depart more widely from the primitive type than do the Anisoptera. From this brief sketch it is evident that these parts will furnish systematic characters which are as yet unused.

For increasing its efficiency, certain methods of bracing the dragon-fly wing in its costal and basal parts have been perfected to a degree surpassing anything to be seen in any other order. The veins of the costal margin are thickened and approximated as usual; but the strong corrugation of the area traversed by them is maintained by their being bound together

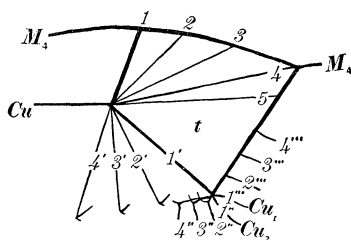


FIG. 65.—Diagram setting forth the behavior of the triangle in the suborder Anisoptera. The heavy lines bound a somewhat primitive triangle. 2, 3, 4, and 5 are stages in the descent of the upper cross-vein which are to be seen in such living genera as *Tetrathemis*, *Anatya*, *Libellula*, and *Tetragoneuria*, respectively. 1', 2', 3', and 4' represent successive stages in the retraction of the cubitus at the triangle, stages seen in the fore wings of *Microdiplax*, *Anatya*, *Sympetrum*, and *Perithemis*, respectively. 1'', 2'', 3'', and 4'' represent stages in the retraction of the base of vein  $Cu_2$  as seen in the fore wings of *Orchithemis*, *Anatya*, *Libellula*, and *Tetragoneuria*. 1''', 2''', 3''', and 4''' represent stages in the ascent of the vein  $Cu_1$  up the outer side of the triangle, stages seen in the hind wings of *Ladona*, *Mesothemis*, *Anatya*, and *Nannodythemis*.

at the nodus, at the stigma, and often toward the base, where certain of the antenodal cross-veins become greatly thickened. These hypertrophied antenodals sometimes (as in *Æschna*) become stout triangular trusses which completely fill, in section, the furrow between the costa and the radius. Toward its base, the wing is braced by two characteristic structures well known in the literature of the Odonata as the *arculus* and the *triangle*. The *arculus* has already been discussed.<sup>1</sup>

*The Triangle.*—The deflection of the cubital trachea, just before its fork, makes a place for the development of the triangle. This is one of the most important

features of the wings in the suborder Anisoptera, to which alone the following remarks will apply. While its stout bound-

<sup>1</sup> *American Naturalist*, vol. xxxii, No. 376, p. 234, Fig. 7.

aries unite strongly the three posterior longitudinal veins, only its inner side is bounded by a principal vein, its anterior and outer sides being formed from two cross-veins approximated upon vein  $M_4$ . Primitively it differed little from an ordinary rectangular cell. The accompanying diagram (Fig. 65) shows the successive positions assumed by its anterior and inner sides

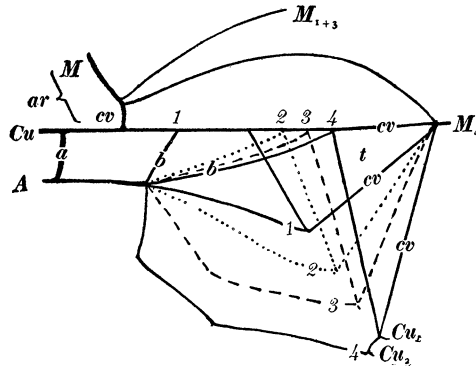


FIG. 66. — Diagram illustrating the procession of the triangle, and the deflection of the second Cu-A cross-vein in the fore wings of Libellulidæ.  $a$ , the first, and  $b$ , the second Cu-A cross-veins; 1, 2, 3, and 4, successive positions.

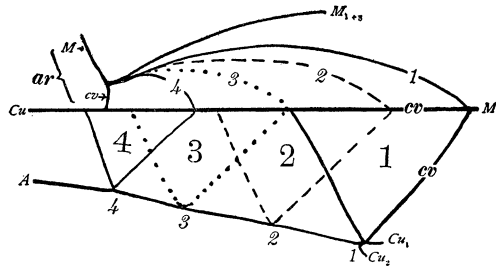


FIG. 67. — Diagram representing the recession of the triangle in the hind wings of the Libellulidæ. 1, 2, 3, and 4, successive stages.

and by the two branches of the cubitus at their departure from it. This epitome of its history presents only steps in its development that are still preserved in the wings of living genera.

In the Libellulidæ differentiation between fore and hind wing has changed the relation between arculus, triangle, and anal vein. Doubtless these were once similarly placed in the two wings, the triangle being a little beyond the arculus, and the anal vein meeting its hind angle in both wings (as, for

instance, at present in *Cordulegaster*). In the fore wing the anal vein has come to connect with the antero-internal angle of the triangle through the deflection of the second cubito-anal cross-vein, and the triangle has proceeded farther from the arcus. Successive steps are shown in the accompanying diagram (Fig. 66). In the hind wing the triangle has receded to the level of the arcus, or even a little farther, by the easy stages shown in the accompanying diagram (Fig. 67), and the second cubito-anal cross-vein has atrophied.

*The Anal Loop.* — There is also in the Anisoptera a strong tendency toward the development in the hind wing of a broadly expanded anal area — an *aéroplane*. This region remains still

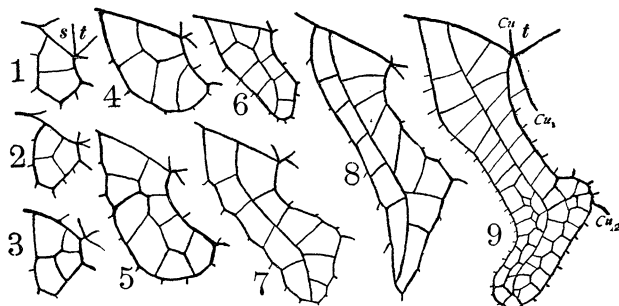


FIG. 68. — Forms of the anal loop in the Anisoptera: 1, anal loop of *Cyclophylla diphylla*; 2, of *Gomphoides stigmatus*; 3, of *Gomphæschna furcillata*; 4, of *Gomphomacromia paradoxa*; 5, of *Syncordulia gracilis*; 6, of *Agrionoptera insignis*; 7, of (?) *Nannophya maculosa*; 8, of *Ephidatia longipes*; 9, of *Hydrobasileus extraneus*.

unexplored territory. It will furnish, however, at least one character of much systematic importance. This is a space included between the first and second principal branches of the anal vein, which we designate as the *anal loop*. Its development is shown in Fig. 61. When developed in the *Æschnidæ* as a distinct enclosure, it is always compact in form, but in the more specialized of the *Libellulidæ* it becomes elongate, then gland-shaped, and then foot-shaped. Fig. 68 shows its more characteristic forms, and gives an idea of its variability within the group.

We have now indicated the homologies of the principal veins: we have briefly discussed the development of a few of the distinctive venational characters of this interesting group;



there is not space for details, but these are the less necessary because the junior author will shortly publish elsewhere an extended paper upon the venation of this order. It may be remarked, however, in passing, that the tendency throughout the order is toward vein multiplication. Additions are made upon both sides of several principal branches, and they conform to no one simple type. These new branches are preceded by tracheæ; but there are other interpolated veins developed for mechanical advantage quite independently of the tracheæ and cutting across them.

The radial sector is unique in form as well as in position.

All the peculiarities of this intricate venation have arisen out of the necessity for making all the veins individually useful: and those dragon flies which have been most successful in differentiating between the added veins are among the fleetest of winged creatures.



## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER IV (*continued*).

#### *The Specialization of Wings by Addition.*

#### IV. THE VENATION OF THE WINGS OF EPHEMERIDA.

THE determination of the homologies of the wing-veins of May-flies appears, at first sight, to be an extremely difficult problem; for the wings of these insects are very different from those of any other order. But, as soon as one understands the ways in which the wings have been modified, it is easy to identify the principal veins.

In this order a marked cephalization of the flight function has taken place, which has resulted in a great reduction of the hind wings of all living forms. In some cases (*Cænis et al.*) this has gone so far that the hind wings are wanting.

In a few genera (*Oligoneura et al.*) both pairs of wings are furnished with but few veins. It requires only a little study, however, to convince one that these genera with few-veined wings are degraded and not generalized. It is in the fore wings of those forms in which many wing-veins have been retained that the homologies of the wing-veins are most easily determined.

Fig. 69 represents the venation of a species which will serve well as a type of the recent May-flies; and the lettering of the figure indicates our conclusions regarding the homologies of the veins. But the most characteristic feature of the wings is not shown in the figure. If the reader will examine one of the larger May-flies, he will see that the corrugation of the wings is much more perfect than in any other order of insects, extending to all parts of the wings.

This fan-like structure of the ephemerid wings has been referred to by many writers. But it is worth while to point

out in this place the degree of perfection that has been reached in the alternation of convex and concave veins. In the accompanying table the names of the convex veins, those veins that follow the crests of ridges, are printed in *Italics*; while the names of concave veins, those veins that follow the furrows, are printed in Roman type.

TABLE OF WING-VEINS OF EPHEMERIDA.

<i>C.</i>	<i>Costa</i>	.	.	.	.	.	.	.	.	.	<i>C.</i>
Sc.	Subcosta	.	.	.	.	.	.	.	.	.	Sc.
<i>R.</i>	<i>Radius</i>	.	.	.	.	.	.	.	.	.	<i>R</i> <sub>1</sub>
											<i>R</i> <sub>2</sub>
											<i>R</i> <sub>3</sub>
											<i>R</i> <sub>4</sub>
											<i>R</i> <sub>5</sub>
Rs.	Radial sector										<i>R</i> <sub>1</sub>
											<i>R</i> <sub>2</sub>
											<i>R</i> <sub>3</sub>
											<i>R</i> <sub>4</sub>
											<i>R</i> <sub>5</sub>
											<i>R</i> <sub>6</sub>
											<i>R</i> <sub>7</sub>
											<i>R</i> <sub>8</sub>
											<i>R</i> <sub>9</sub>
											<i>R</i> <sub>10</sub>
											<i>R</i> <sub>11</sub>
											<i>R</i> <sub>12</sub>
											<i>R</i> <sub>13</sub>
											<i>R</i> <sub>14</sub>
											<i>R</i> <sub>15</sub>
											<i>R</i> <sub>16</sub>
											<i>R</i> <sub>17</sub>
											<i>R</i> <sub>18</sub>
											<i>R</i> <sub>19</sub>
											<i>R</i> <sub>20</sub>
											<i>R</i> <sub>21</sub>
											<i>R</i> <sub>22</sub>
											<i>R</i> <sub>23</sub>
											<i>R</i> <sub>24</sub>
											<i>R</i> <sub>25</sub>
											<i>R</i> <sub>26</sub>
											<i>R</i> <sub>27</sub>
											<i>R</i> <sub>28</sub>
											<i>R</i> <sub>29</sub>
											<i>R</i> <sub>30</sub>
											<i>R</i> <sub>31</sub>
											<i>R</i> <sub>32</sub>
											<i>R</i> <sub>33</sub>
											<i>R</i> <sub>34</sub>
											<i>R</i> <sub>35</sub>
											<i>R</i> <sub>36</sub>
											<i>R</i> <sub>37</sub>
											<i>R</i> <sub>38</sub>
											<i>R</i> <sub>39</sub>
											<i>R</i> <sub>40</sub>
											<i>R</i> <sub>41</sub>
											<i>R</i> <sub>42</sub>
											<i>R</i> <sub>43</sub>
											<i>R</i> <sub>44</sub>
											<i>R</i> <sub>45</sub>
											<i>R</i> <sub>46</sub>
											<i>R</i> <sub>47</sub>
											<i>R</i> <sub>48</sub>
											<i>R</i> <sub>49</sub>
											<i>R</i> <sub>50</sub>
											<i>R</i> <sub>51</sub>
											<i>R</i> <sub>52</sub>
											<i>R</i> <sub>53</sub>
											<i>R</i> <sub>54</sub>
											<i>R</i> <sub>55</sub>
											<i>R</i> <sub>56</sub>
											<i>R</i> <sub>57</sub>
											<i>R</i> <sub>58</sub>
											<i>R</i> <sub>59</sub>
											<i>R</i> <sub>60</sub>
											<i>R</i> <sub>61</sub>
											<i>R</i> <sub>62</sub>
											<i>R</i> <sub>63</sub>
											<i>R</i> <sub>64</sub>
											<i>R</i> <sub>65</sub>
											<i>R</i> <sub>66</sub>
											<i>R</i> <sub>67</sub>
											<i>R</i> <sub>68</sub>
											<i>R</i> <sub>69</sub>
											<i>R</i> <sub>70</sub>
											<i>R</i> <sub>71</sub>
											<i>R</i> <sub>72</sub>
											<i>R</i> <sub>73</sub>
											<i>R</i> <sub>74</sub>
											<i>R</i> <sub>75</sub>
											<i>R</i> <sub>76</sub>
											<i>R</i> <sub>77</sub>
											<i>R</i> <sub>78</sub>
											<i>R</i> <sub>79</sub>
											<i>R</i> <sub>80</sub>
											<i>R</i> <sub>81</sub>
											<i>R</i> <sub>82</sub>
											<i>R</i> <sub>83</sub>
											<i>R</i> <sub>84</sub>
											<i>R</i> <sub>85</sub>
											<i>R</i> <sub>86</sub>
											<i>R</i> <sub>87</sub>
											<i>R</i> <sub>88</sub>
											<i>R</i> <sub>89</sub>
											<i>R</i> <sub>90</sub>
											<i>R</i> <sub>91</sub>
											<i>R</i> <sub>92</sub>
											<i>R</i> <sub>93</sub>
											<i>R</i> <sub>94</sub>
											<i>R</i> <sub>95</sub>
											<i>R</i> <sub>96</sub>
											<i>R</i> <sub>97</sub>
											<i>R</i> <sub>98</sub>
											<i>R</i> <sub>99</sub>
											<i>R</i> <sub>100</sub>

One of the most characteristic features in the venation of the wings of May-flies is that the radial sector plays the part of a principal vein; it originates near the base of the wing; and, as a rule, it is detached, in the adult, from the main stem of the radius.<sup>1</sup> For this reason it is given the position of a principal vein in the table.

If this modification be made, it will be seen that, when the principal veins are considered, there is a strict alternation of convex and concave veins; and that in the case of the forked veins (the radial sector, the media, and the cubitus) the principal branches of a vein are of the same nature as the main stem.

It will also be seen that this alternation of convex and concave veins exists in the distal portion of the wing. In those

<sup>1</sup> In certain Plecoptera and Trichoptera the radial sector of the hind wings is detached in a similar manner.

cases where a vein has an even number of branches (the radial sector and the cubitus) the alternation has been attained by the development of an accessory vein. These are indicated in the table as chief accessory veins, and are lettered *i* in the figure. Many other accessory veins are developed at the margin of the wing in a more or less irregular manner; but whenever a second accessory vein extends far into the disk of the wing it is accompanied by a third, one being convex, the other concave. The anal area of the wing, where the accessory veins are more of the nature of braces, like cross-veins, is not included in this statement, nor in that which follows.

Correlated with the development of a triangular form of wing, which involves an expanding of its outer margin, is the fact that the accessory longitudinal veins are all added distally in the May-flies. But the method of development of these veins appears to be radically different from what it is in the Neuroptera.<sup>1</sup> There the accessory longitudinal veins are preceded by tracheæ, which arise as fine twigs at the tips of older tracheæ, and which in the course of phylogenetic development branch off from the parent tracheæ farther and farther from the margin of the wing, thus making room for the development of other twigs. Here, in the May-flies, the accessory longitudinal veins are evidently thickened folds, which arise more or less nearly midway between other veins. A similar thickening of a fold occurs in the Diptera, where, in certain Asilidæ, the anal furrow is vein-like in structure.

A fact of prime importance in the study of the homologies of the wing-veins of May-flies is that the corrugations of the wing are the most persistent features of it. Hence the most important criterion for determining the homology of a vein is whether it is a concave or a convex one. The basal connections of the veins are very inconstant, and are often misleading. We have already referred to the separation of the radial sector from the main stem of the radius in the adult (its true origin is easily seen when the tracheation of the wings of certain nymphs is studied); and other separations and secondary attachments are common. A good illustration is furnished by the wings

<sup>1</sup> See *American Naturalist*, vol. xxxii, pp. 771, 772.

represented by Fig. 69. In the hind wing, vein  $Cu_2$  is apparently a branch of the first anal vein (marked  $A$  in the figure); but in the fore wing, which is less modified, its primitive connection is preserved; although even here a prominent bend has brought it near to the anal vein, and only a step more would be required, the fading out of the basal section, to reach

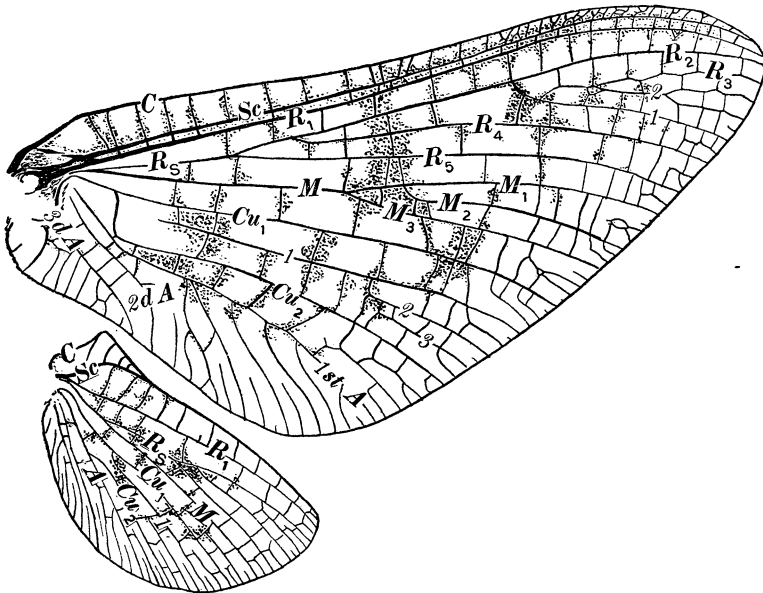


FIG. 69. — Wings of *Ephemera*.

the condition attained in the hind wing. But the concave nature of this vein in the hind wing indicates its homology in spite of its misleading basal connection.

It should be remembered that the convex or concave nature of a vein is the result of a corrugation of the wing and not the cause of this corrugation. The theory of Adolph that the two sets of veins have a different ontogenetic development has absolutely no foundation in fact, as will be seen when we come to study the development of wing-veins, and as was suspected by Brauer and Redtenbacher.<sup>1</sup>

The primitive insect wing was doubtless flat. It makes no

<sup>1</sup> *Zoologischer Anzeiger*, 1888, p. 443.

difference, so far as this point is concerned, whether we believe that the wing is a modified tracheal gill or a transformed parachute-like expansion of the body wall. In either case it is highly improbable that it was fanlike at first. It was not until the wing became an organ of flight that a corrugation of it was beneficial; and even then this corrugation did not spring into existence suddenly, only to be lost in most of the orders of insects; as must be inferred, if we accept the theory of Adolph, that the wing of a May-fly represents the primitive type of this organ.

The stiffening of the costal margin of the wing by the formation of a subcostal furrow has been attained in most of the orders of insects; and in several of them the formation of folds has extended, to a greater or less degree, to other parts of the wing. But, as a rule, this method of specialization has not been the most important one in perfecting the wing. In the Odonata it has been carried farther than elsewhere, among living insects, except in the Ephemera. But in the Odonata it has been supplemented by other methods of specialization, already discussed, with the result that an exceedingly efficient organ of flight has been developed in that order; while in the Ephemera the cephalization of the flight function and the corrugating of the wings have been the chief lines along which specialization has extended. The former has doubtless added much to the efficiency of the wings; but a too close adherence to the latter method of specialization has resulted in the formation of a rather indifferent organ; although it is the most perfect development of its peculiar type.

We have studied the tracheation of many nymphs of May-flies, but with results much less satisfactory than those we have reached in the study of other orders of insects with many-veined wings. In all nymphs of May-flies that we have examined, a greater or less reduction of the tracheæ appears to have taken place; and in many of them a large proportion of the longitudinal veins contain no tracheæ. And, too, the presence or absence of a trachea in a vein appears to have little significance. As an example of this the wings of two nymphs are before the writer, in which the venation is so similar that there

is not the slightest difficulty in tracing the homologies of the veins. In one the radial sector and the media contain well-preserved tracheæ; in the other there is not the slightest trace of a trachea in these veins. On the other hand, in the latter the cubital trachea is forked, one of the branches traversing vein  $Cu_2$ ; while in the former the cubital trachea is simple, there being not the slightest indication of a trachea in vein  $Cu_2$ .

The basal connections of the trachea of the wing are very different from what we have seen elsewhere. In the Plecoptera there are two distinct groups of tracheæ which enter the wing;<sup>1</sup> the same is true of certain cockroaches;<sup>2</sup> in all other forms

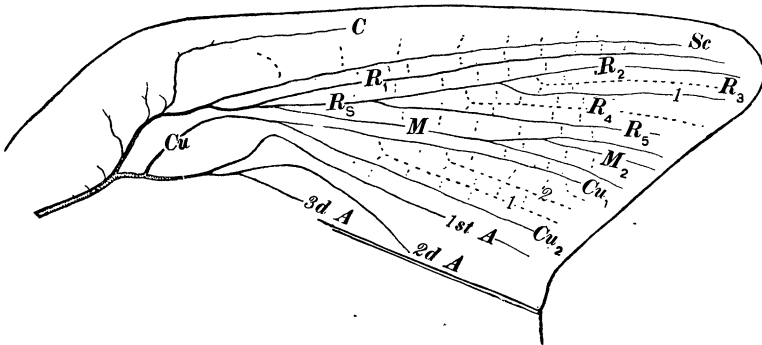


FIG. 70.—The tracheation of a wing of a May-fly nymph.

that we have studied, except the May-flies, a transverse basal trachea connects these two groups, and from this transverse trachea (transverse in relation to the wing, but longitudinal in relation to the body) the principal tracheæ of the wing extend more or less nearly at right angles to it.<sup>3</sup> In the May-flies a single trachea arises from the principal longitudinal trachea of one side of the thorax, and, after giving off a branch to the corresponding leg, passes directly to the base of the wing. Here it divides into several branches which continue in approximately the same direction and become the principal tracheæ of the wing.

In some cases this trachea extends into the wing before it divides. But in other forms, which we regard as more general-

<sup>1</sup> *American Naturalist*, vol. xxxii, p. 238, Fig. 8; p. 239, Fig. 9.

<sup>2</sup> *Loc. cit.*, p. 773, Fig. 56.

<sup>3</sup> *Loc. cit.*, p. 772, Fig. 54.



ized, it separates into two trunks in the thorax near the base of the wing (Fig. 70); from one of these arises the costo-radial group of tracheæ, and from the other the cubito-anal group.

Fig. 70 will serve to illustrate what may be considered the type of tracheation of the wings in this order. It was made from a study of the nymphs referred to above. The positions of those longitudinal veins that contained no tracheæ in these nymphs are indicated by dotted lines.

The discussion of the venation of the wings of Ephemera brings up the question of the venation of the primitive insect wing. For, in several of the more important papers on the homologies of wing-veins, it has been assumed that the wings of May-flies resemble closely the wings of the primitive winged insect.

The great preponderance of the many-veined type among the insect wings that have been found in the Carboniferous rocks has doubtless strengthened the quite generally accepted view that the primitive winged insect had many wing-veins. Thus Redtenbacher states:<sup>1</sup>

The geologically older Orthoptera and Neuroptera show a much richer venation than the Coleoptera, Lepidoptera, Hymenoptera, and Diptera; likewise among the Rhyncota, the oldest forms, the Cicadas and the Fulgoridæ, possess much more numerous veins than the Hemiptera. There is apparently, then, no doubt that the oldest insect forms were provided, to a certain extent, with a superfluity of veins, and that, in the course of development, all the superfluous veins disappeared by reduction, and in this way a simple system of venation was brought about.

But we have shown that all the existing types of insect wings can be derived from one in which there are but few wing-veins — our hypothetical type, already figured several times. The deviations from this type in the more generalized members of the greater number of the orders of insects is slight. And we have pointed out the ways in which it is being modified, on the one hand by the coalescence of veins, and on the other by the development of accessory veins. While this is easy to understand, it is very difficult to conceive how the wings of the Lepidoptera, Diptera, and Hymenoptera could have been

<sup>1</sup> *Annalen des k. k. nat. Hofmuseums*, Bd. i, p. 153.

evolved from a wing of either the ephemerid or neuropterous type. After a wing had been strengthened by many cross-veins, it is not probable that these should disappear with the exception of the few to which we have applied names<sup>1</sup> in so many different orders, in so nearly an identical manner. Forms with reduced venation occur in most of the orders, but the results of these independent reductions differ greatly from each other. It is necessary, therefore, to examine again the paleontological evidence.

The great preponderance of many-veined wings in the Carboniferous rocks is probably due to the fact that doubtless then, as now, insects with many wing-veins were the ones that lived near water, and were, therefore, the ones most likely to be preserved as fossils.

Another point which should be taken into account is that, notwithstanding the great antiquity of the Carboniferous times, it was a comparatively late period in the history of insects, for winged insects appeared in the Silurian. We are carrying our investigations back only a step, although it is a long one, towards the period when wings were first developed by studying Carboniferous fossils.

Unfortunately, our knowledge of Silurian insects is meager. Moberg has figured an insect from the upper part of the lower Silurian; and Brongniart has figured and described a wing from the middle Silurian sandstone of Calvados, France. This we believe is all that is known regarding the insect fauna of the Silurian; and when we take into account the immensity of the period of time occupied by the deposition of the Silurian rocks, we are forced to admit that we know almost nothing regarding the older insects.

Of the Devonian insects, the remains of several are known. Those which are best preserved are *Homothetus fossilis* (Fig. 71), *Xenoneura antiquorum* (Fig. 72), and *Platephemera antiqua* (Fig. 73). (The figures given here are reproduced from Plate VII of Mr. Scudder's *Pretertiary Insects*.) A glance at these figures will convince the reader that the insects of the Devonian times varied greatly in the structure of their wings. For

<sup>1</sup> *American Naturalist*, vol. xxxii, pp. 233, 234.

these three insects differ as much from each other as do the more generalized members of widely separated orders of living insects. Evidently, comparatively high specializations in widely

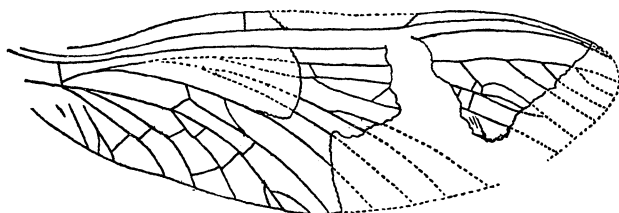


FIG. 71. — *Homothetus fossilis*.

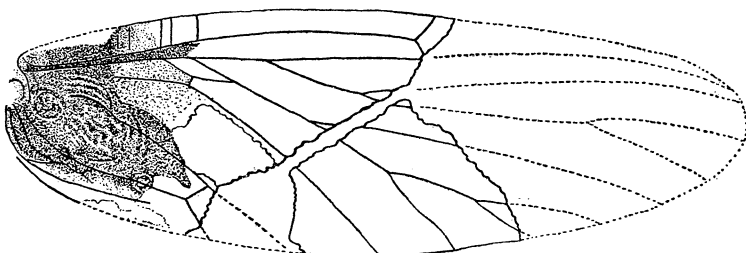


FIG. 72. — *Xenoneura antiquorum*.

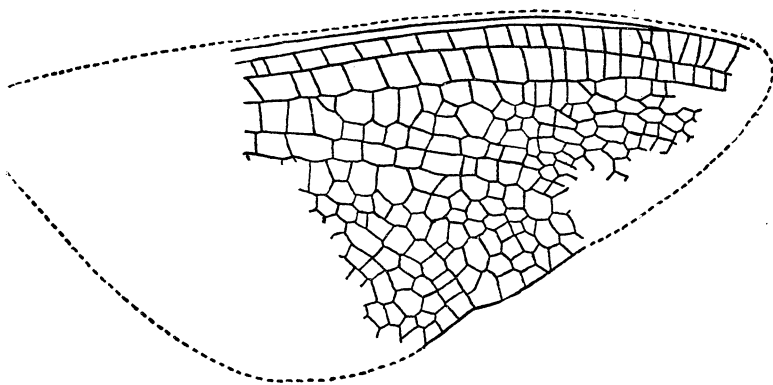


FIG. 73. — *Platephemera antiqua*.

different directions had been attained already at that early time. But the point to which we wish to call especial attention is that, of the three better-preserved Devonian insects, one (*Xenoneura*) had but few wing-veins. And when we consider the

slight amount of data that we have, the numerical preponderance of the many-veined type has no significance.

It is easy to conceive of the development of the wings of all living insects from forms allied to *Xenoneura*, by the different methods of specialization which we have pointed out; for it will be seen that the wing of this insect closely resembles our hypothetical type. And we can say, therefore, that the paleontological evidence does not contradict the conclusions drawn from a study of the ontogeny of living forms.

## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER IV (*Concluded*).

#### *The Specialization of Wings by Addition.*

#### V. THE TRACHEATION OF THE WINGS OF ORTHOPTERA.

THE study of the tracheation of wings of orthopterous nymphs was undertaken merely for the purpose of determining the homologies of the wing-veins in this order; but some of the results attained have a much wider bearing, giving a hint as to the position of this order in the class Insecta. For this reason, after setting forth the conclusions regarding the homologies of the tracheæ of the wings, a brief discussion of the taxonomic bearing of some of these conclusions will be given.

*The Homologies of the Principal Tracheæ of the Wings of Orthoptera.* — In this investigation representatives of the Blattidæ, Acrididæ, Locustidæ, and Gryllidæ have been examined; no living nymphs of members of the Mantidæ nor of winged Phasmidæ were studied. It is not probable, however, that these will present serious difficulties.

The most uniform characteristic of the wings of the four families studied is the structure of the anal area of the hind wings. For this reason we will begin our description of the tracheation of the wings with this area and proceed cephalad.

In the Orthoptera the anal area of the hind wings is broadly expanded and fanlike in form. The first anal trachea is simple (Figs. 74–78 *A*); the second and third anal tracheæ coalesce for a distance and then separate into several tracheæ, each of which traverses a convex vein of the fanlike portion of the wing. Sometimes, as in the wing of an Acridid, represented by Fig. 75, the common trunk of these two tracheæ divides into two large trunks, which probably correspond to the second and third

anal tracheæ respectively; but in most cases this division is not clearly indicated.

In many of the saltatorial Orthoptera the anal area of the hind wings bears a striking resemblance to the wings of Ephemeroidea, there being a regular alternation of convex and concave veins. In these cases the concave veins are evidently a later development than the convex veins. The increase in the number of the branches of the anal tracheæ takes place at the cau-

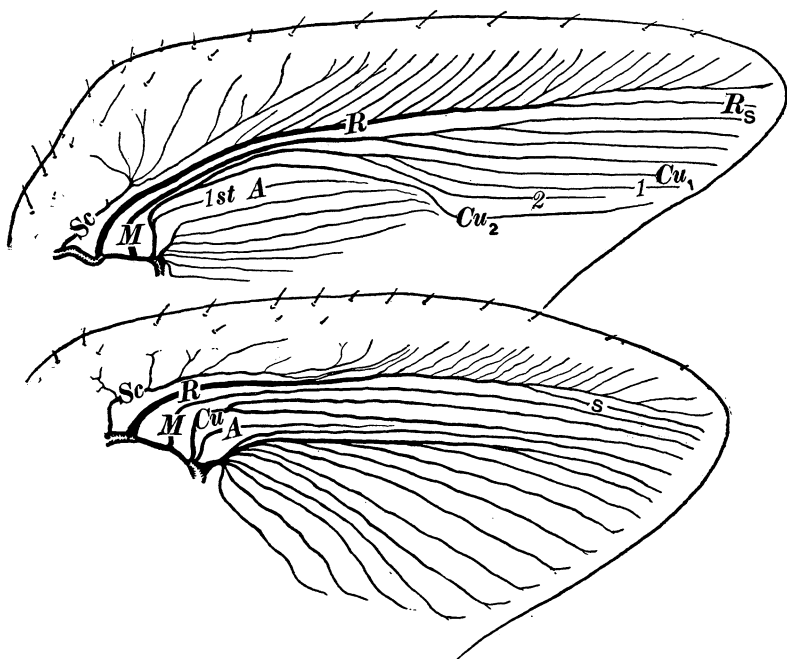


FIG. 74. — Wings of a nymph of a cockroach.

dal end of the series, and about each added trachea a convex vein is developed. It is only after the space between two of these convex veins becomes wide enough to admit of a fold in the wing that a concave vein is developed, and this development takes place in the same manner as in the Ephemeroidea. In some cases, as in the hind wings of *Scudderia* (Fig. 77), a tertiary set of anal veins is developed; these extend only a short distance from the margin of the wing, and increase the resemblance of this area to an Ephemeroidea wing.

The cubital trachea of the hind wings varies greatly in form, even within the limits of a single family. In the Acrididæ it is sometimes reduced to an unbranched condition (Fig. 75 *Cu*); in all of the Locustidæ known to us it retains the primitive two-branched condition (Fig. 76); in *Œcanthus* (Fig. 78) there is a single accessory cubital trachea; while in certain cockroaches, not figured here, vein *Cu*<sub>1</sub> is pectinately branched.

Similar variations in the number of branches of each of the other principal tracheæ of the hind wings occur. It is not

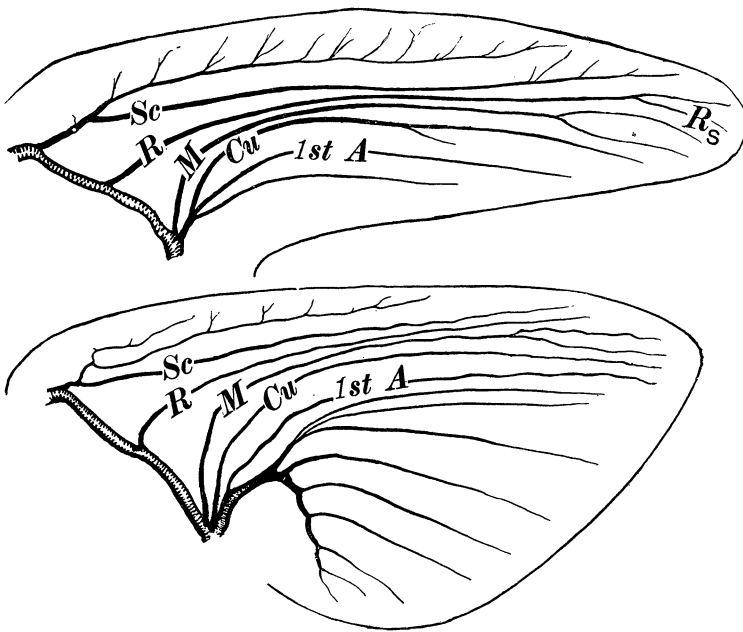


FIG. 75. — Wings of an Acridid nymph.

necessary to point them out in detail, as they are sufficiently indicated by the lettering of the figures. The most striking features are the reduction of the radius, the radial sector being at most unimportant, and in some cases entirely wanting, and the loss of the costal trachea.

In the fore wings the anal area is variously modified in the different members of the order. In the female *Œcanthus* (Fig. 78) it nearly retains its primitive form; in the Acridid,

represented by Fig. 75, a reduction of this area has taken place; while in the *Blattidæ* (Fig. 74) the three anal tracheæ are pre-

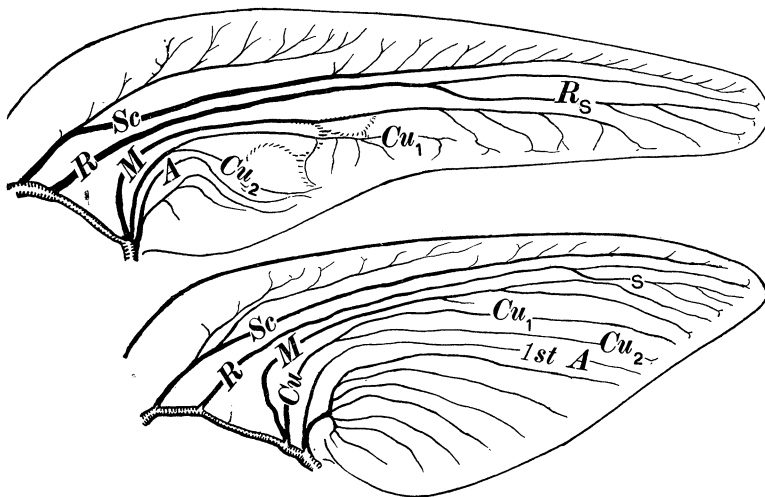


FIG. 76. — Wings of a nymph of *Conocephalus*.

served and the second and third have been specialized by addition, these tracheæ consisting of several parallel branches.

The cubital trachea is reduced to a nearly simple condition

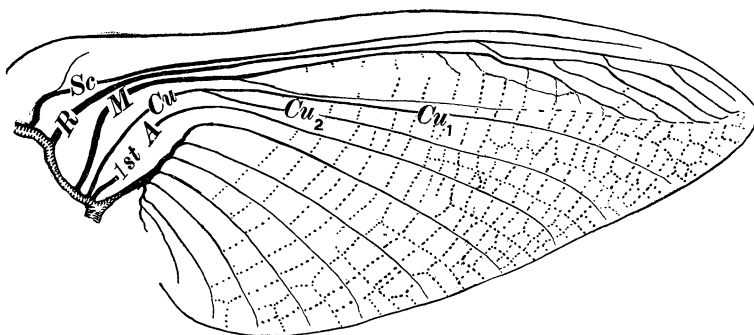


FIG. 77. — Hind wing of a nymph of *Scudderia*. Dotted lines indicate adult venation in part.

in the *Acridid* (Fig. 75); but in the other forms examined accessory tracheæ are developed on the caudal side of trachea *Cu*<sub>1</sub>.

In the males of the *Locustidæ* (Fig. 76) and of the *Gryllidæ* (Fig. 79) the formation of a musical organ has been attained



by a modification of the cubital and anal areas. An extreme case of this is furnished by the male *Æcanthus* (Fig. 79). The principal vibrating area of the wing lies between the branches of the cubitus, which diverge widely in this sex.

A study of the musical organs of adult Orthoptera throws light on the nature of the anal furrow. In the female this furrow lies between the cubitus and the first anal vein; but in the males of the Locustidæ and Gryllidæ the anal furrow crosses

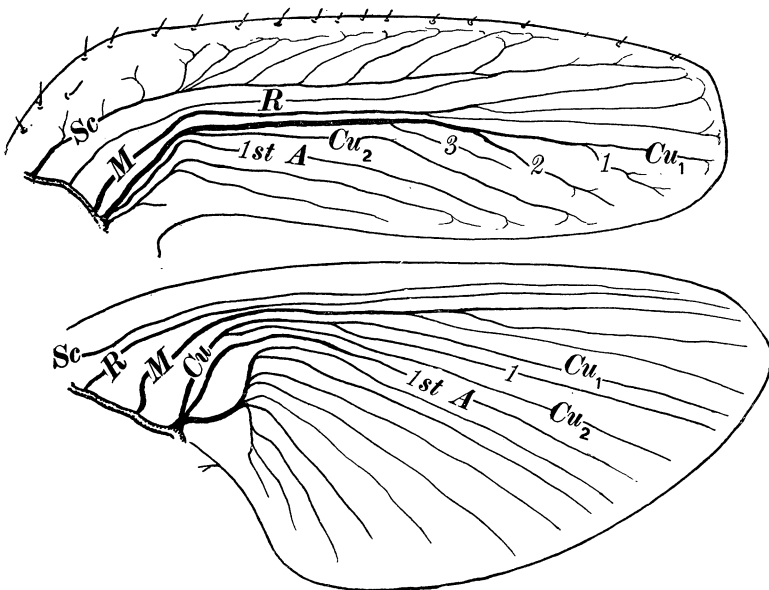


FIG. 78. — Wings of a female nymph of *Æcanthus*.

vein *Cu*<sub>2</sub>. It is evident, therefore, that this furrow is merely a fold in the adult wing, and that its position is variable. It has already been shown<sup>1</sup> that in the Heteroptera, when an anal furrow is developed, it is in front of the cubitus, instead of in the more usual position between the cubitus and the first anal vein.

Although the wings of the two sexes of *Æcanthus* present a very different appearance, there is really a very close correspondence in the tracheation (and consequently in the vena-

<sup>1</sup> *American Naturalist*, vol. xxxii, p. 252.

tion) of the two, as can be seen by comparing the lettering of Figs. 78, 79; the same number of anal veins and of accessory cubital veins exist in the two sexes.

The lettering of the figures will serve to show the striking differences in the development of the remaining veins in different members of the order. Thus, for example, while the radius is the most prominent vein in the fore wing of the cockroach (Fig. 74), in *Æcanthus* (Figs. 78, 79) it is the least developed

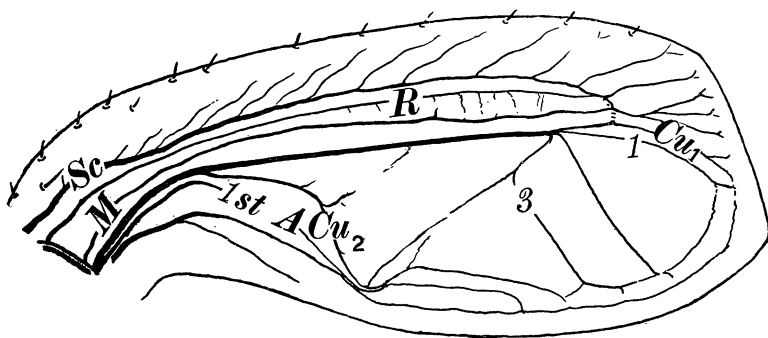


FIG. 79. — Fore wing of a male nymph of *Æcanthus*.

of the principal veins; or, to take another example, the subcosta is greatly reduced in the cockroach (Fig. 74), while in the Acridid (Fig. 75) and in the Locustid (Fig. 76) it is as well developed as any other vein.

In none of the Orthoptera that we have examined is the costal trachea distinctly preserved. Frequently, as in the Acridid (Fig. 75) and in the Locustid (Fig. 76), there is a prominent branch of the subcostal trachea which simulates a costal trachea; but that this is merely an overgrown branch of the subcostal trachea is evident when a series of forms are studied; in the hind wing of *Conocephalus* (Fig. 76) there are two such branches.

It will be remembered that in our hypothetical type the subcosta is two-branched, and that the branches are designated as  $Sc_1$  and  $Sc_2$  respectively. A good example of this typical branching of the subcosta is afforded by *Nemoura*.<sup>1</sup> But there

<sup>1</sup> *American Naturalist*, vol. xxxii, p. 238, Fig. 8.

are no indications that the primitive branching has been retained in the Orthoptera; here, when the two-branched condition exists, it is a secondary development; it would be misleading, therefore, to designate these branches as  $Sc_1$  and  $Sc_2$ , for they do not correspond to the branches so designated in other orders. In this case the branch, or branches, of the subcostal trachea are merely accessory branches, like the accessory branches developed on other principal tracheæ.

Although the costal trachea has been lost, the thickening of the costal margin of the wing should be called the costal vein; for it is still the vein that was formed about the costal trachea in the beginning.

The few illustrations given here will show how easily the homologies of the tracheæ of the wings of orthopterous nymphs, and consequently of the veins that are formed about them, can be determined. But if one studies only the wings of adults, where many cross-veins have been developed, and where the basal connections of the principal veins are obscured, it is extremely difficult to determine these homologies. It is also evident that the wings of these insects present many characters which are easily available for taxonomic purposes.

*The Position of the Orthoptera in the Class Insecta as indicated by the Tracheation of the Wings.* — The making of genealogical trees does not fall within the scope of the present series of papers. Our object has been to learn in what ways wings have been modified in order to determine the homologies of the wing-veins. It is obvious that this had to be done before the characters presented by the wings could be used intelligently in working out the phylogeny of the orders. Now that this has been accomplished, it would be possible to propose a provisional classification of insects based on the characters of the wings; but we feel that it is much better to wait till the results we have attained can be correlated with similar studies of other organs. There is, however, one character in the tracheation of the wings to which it seems worth while to call attention now.

In most insects the principal tracheæ of the wings form two quite distinct groups. These we have already designated as the

costo-radial and the cubito-anal groups respectively.<sup>1</sup> To the former belong the costa, the subcosta, and the radius; to the latter, the cubitus and the anal veins. These groups find their attachment to the main tracheal system of the body at points wide apart; in the Perlid genus, *Capnia*, the former group springs from the dorsal lateral trunk, the latter from ventral lateral trunk of the thorax.<sup>2</sup> Even in such groups as Trichoptera, Hymenoptera, and Diptera, where great reduction has taken place, the persisting tracheæ clearly represent these two groups.

The media is sometimes a member of the costo-radial group (Fig. 80) and sometimes of the cubito-anal group (Fig. 76). In

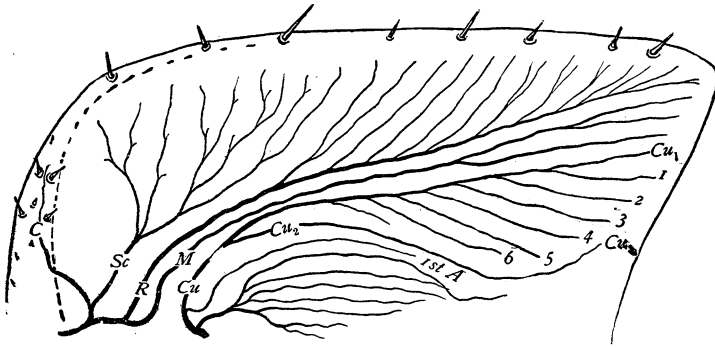


FIG. 80. — Fore wing of a nymph of a cockroach.

certain forms, however, the media arises midway between these two groups from a transverse basal trachea which joins them, suggesting at once the possibility of its migration from one group to the other. Since there is no evidence of its having entered the wing independently, to which of the two groups did it belong in the primitive winged insect? The answer lies (1) in the rank of the insects showing the different conditions, and (2) in the ontogeny of the media itself.

(1) Only in the Plecoptera and in some of the Blattidæ does the media clearly belong to the costo-radial group, and in these there is no basal transverse trachea connecting the two groups;

<sup>1</sup> *American Naturalist*, vol. xxxii, p. 88.

<sup>2</sup> A fact of no little interest in its relation to the question of a former respiratory function in these or closely related parts; since tracheal gills are commonly joined to both longitudinal lateral trunks, securing, doubtless, better distribution of the air.

in all other insects we have studied, the two groups are connected and the media is either joined to the cubito-anal group or arises from the transverse basal trachea. No one will hesitate to believe that the Plecoptera and the Blattidæ are the ones more likely to have retained the more primitive structure.

(2) We have previously shown<sup>1</sup> that in a Cicada nymph one-third grown the medial trachea springs from the transverse basal trachea midway between the radial and the cubital tracheæ, while in the grown nymph it has reached the cubital trachea. In most insects of which we have had nymphs of various ages we have observed the same direction of migration; never any migration in the opposite direction.

From this it follows that, in arranging the orders of winged insects in an ascending series, if we take into account only the structure of the wings, the Plecoptera should be placed first; for this order, as a whole, retains the primitive condition of the basal connections of the wing tracheæ. Next to this in degree of divergence from the primitive wing type stand the Orthoptera, with the Blattidæ the lowest of the series of orthopterous families; for in this family alone is the primitive condition of the basal connections of the wing tracheæ retained.

In this connection attention should be called to the striking similarity of the anal area of the hind wings in the Orthoptera and in the Plecoptera; in both cases the fanlike portion is supported by the second and third anal veins, while the first anal vein remains simple.

An understanding of the nature of the changes that are taking place in the basal connections of the wing tracheæ renders this region of the wing a very instructive one. Let us examine again the figures herewith given: In the wing of a cockroach, represented by Fig. 80, the primitive type is retained, the medial trachea is a member of the costo-radial group, and there is no transverse basal trachea; while in the wings represented by Fig. 74 the basal trachea is well developed, and the medial trachea has begun its migration toward the cubito-anal group, but it still arises from the basal trachea. In all other forms here figured the base of the medial trachea has nearly or quite

<sup>1</sup> *American Naturalist*, vol. xxxii, p. 249.

reached the cubital trachea and usually coalesces to a greater or less extent with it. An extreme case of this migration is illustrated by *Xiphidium* (Fig. 81). And here there appears to be a reduction of the transverse basal trachea. It has served its purpose, and, like an abandoned road, is disappearing from view. It will not be surprising if Locustid nymphs are found

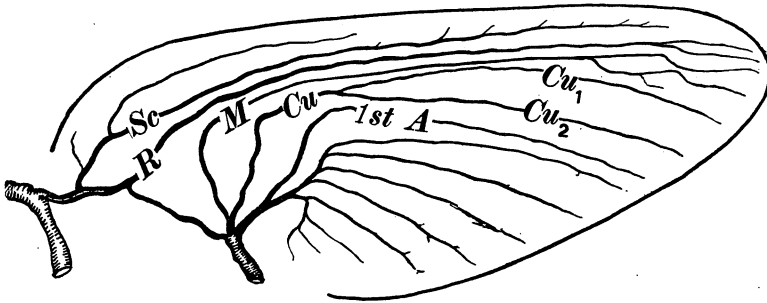


FIG. 81. — Hind wing of a nymph of *Xiphidium*.

in which this connection between the two groups is lost, but the presence of the medial trachea in the cubito-anal group will show it to have existed.

In the Acridid, represented by Fig. 75, the radial trachea is following the medial in its migration; this is indicated well by the curve near the base of the radial trachea in the hind wing.

#### VI. CONCLUSION OF CHAPTER IV.

In this and the preceding chapter we have furnished data for determining the homologies of the veins in each of the orders of winged insects except the Euplexoptera, Mecaptera, Isoptera, and the Physopoda. Of the first two we have been unable to procure immature stages; it is not probable, however, that they will present serious difficulties when they are studied. Of the Isoptera we have examined nymphs of two genera, *Termes* and *Termopsis*, but we wish to examine other forms before publishing conclusions. In all of the Physopoda that we have seen, the tracheation of the wings is so reduced that we have been unable to determine definitely the homologies of the few remaining tracheæ. We therefore close at this point our discussion of this phase of the subject and pass to a study of the beginning of wings.

# THE AMERICAN NATURALIST

---

---

VOL. XXXIII.

November, 1899.

No. 395.

---

---

## THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

### CHAPTER V.

#### *The Development of Wings.*

##### I. FIRST APPEARANCE, POSITION, AND GROWTH OF WINGS.

THE development of wings is one of the many subjects of biologic study which have been first undertaken in their more difficult phases. The internal processes concerned in the making of an insect wing were first studied by Weismann in the Diptera,<sup>1</sup> and in those Diptera in which conditions are most difficult of interpretation. One by one forms of less complexity have been studied, and a rational account of the process of wing development has at length found its way into several textbooks. The process is still most fully illustrated, however, by studies of representatives of the two groups which are least typical for insects as a whole, the Diptera and the Lepidoptera. Rehberg's inconclusive paper on wing development in *Blatta*

<sup>1</sup> Weismann, A. *Zeit. wiss. Zool.*, vol. xiv (1864), pp. 187-336.

*germanica*<sup>1</sup> remains the only considerable attempt to study the making of the wing in an insect with incomplete metamorphosis. In this chapter we give the results of some studies in which we have endeavored to follow the phylogenetic order of wing development.

It is not necessary to trace in this place the steps by which the present state of knowledge of wing development has been

reached; for this has been well done by several writers. Among the more complete of these summaries are those of Gonin<sup>2</sup> and of Pratt.<sup>3</sup>

Neither does it seem desirable to enter into a detailed discussion of controverted points, our object being merely to state what is definitely known on this subject, and to add the results of some of our own investigations.

It is well known that the wings of insects arise as sac-like folds of the body wall of the second and third thoracic segments. These folds first appear at the point where the suture between the tergum and the pleurum later develops. In most insects with incomplete metamorphosis they

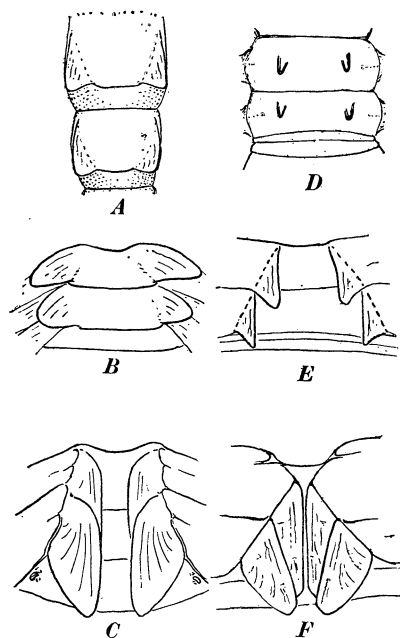


FIG. 82. — Wings of nymphs: *A*, of a stone fly (*Capnia*); *B* and *C*, of a grasshopper; *D*, *E*, and *F*, of a dragon-fly. In the four lower figures the dorsal half of the body of the nymph is represented as spread out flat. Figures *B* and *E* are from nymphs one third grown; and *C* and *F* from nymphs that were three fifths grown.

are so directly continuous with the tergum and become so solidly chitinized with it that they have generally been interpreted as outgrowths from its caudo-lateral margin (Fig. 82, *A*, *B*).

<sup>1</sup> Rehberg, A. *Jahrb. d. k. Gymn. zu Marienwerder*, 1886.

<sup>2</sup> *Bull. de la Soc. Vaud. des Sci. Nat.*, vol. xxi, pp. 90-98.

<sup>3</sup> *Psyche*, vol. viii (1897), pp. 15-30.



In the Plecoptera, Ephemerida, Hemiptera, Blattidæ, *et al.*, the external changes during growth are comparatively slight— increase in size and internal differentiation, and the development of the veins and of the basal articulations. In the more specialized Orthoptera there occurs the well-known reversal of position of the wings at the last molt. In the Odonata there are the noteworthy differences that the wings arise in an erect position upon the body wall, and at midway the length of their respective segments, and not from the hind margin (Fig. 82, *D*). They appear at a time when the tergum and the pleura are very

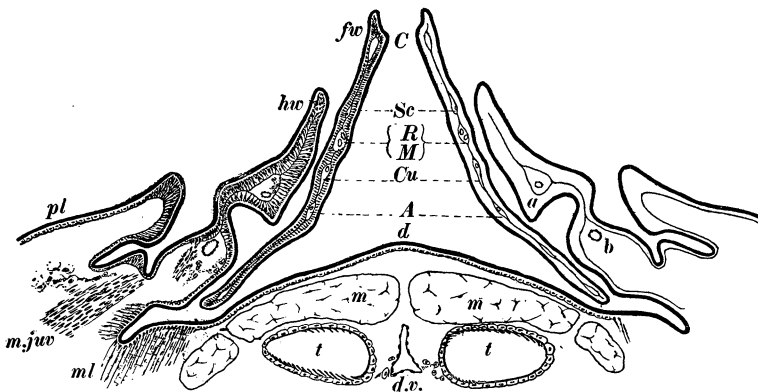


FIG. 83. — Dorsal part of a transverse section of a nymph of *Celithemis elisa*, one third grown : *d*, dorsum; *pl*, pleurum; *d.v.*, dorsal vessel; *t, t*, tracheæ; *m, m*, muscles in cross-section; *ml*, muscles in longitudinal section; *m.juv*, developing muscle of the wing; *fw*, fore wing; *a* and *b*, the cut ends of the basal transverse trachea of the hind wing; *C*, costa; *Sc*, subcosta; *RM*, the coalesced radius and media; *Cu*, cubitus; *A*, anal vein.

little chitinized, and are hardly more identified with one than with the other. Later, as in the saltatorial Orthoptera, owing to a rapid growth of the pleura, especially at the wing bases, they are pushed over upon the dorsum and lie in an inverted position (Fig. 82, *E, F*), to be righted only at the final transformation.

Fig. 83 shows the relations of parts in a dragon-fly nymph one third grown. It represents a partial cross-section passing through the posterior part of the basal attachments of the hind wings and through the fore wings just before the arcus. In the hind wings are seen (*a, b*) the cut ends of the transverse

basal trachea. In the fore wings the tracheæ in the vein cavities are seen in section. The pleura (*pl*) are seen overlying the bases of the wings.

It is interesting to follow the basement membrane of the hypodermis throughout the section, noting how the hypodermal cells are elongated in certain parts, rounding out the sharp

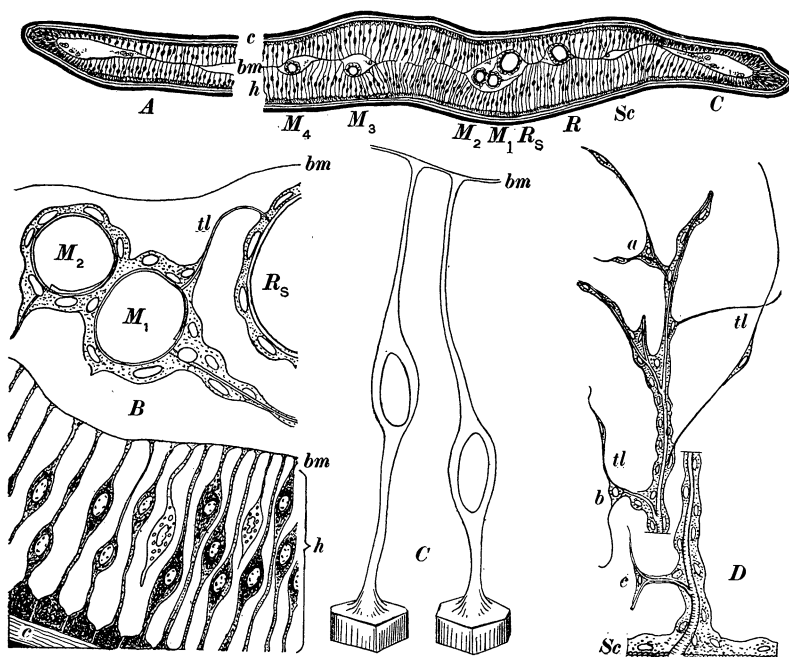


FIG. 84.—*A*, cross-section of a fore wing (in part omitted) of a nymph, two thirds grown, and recently molted, of *Anax junius*; *c*, cuticle; *bm*, basement membrane; *h*, hypodermis; the veins of the wing are designated by the usual lettering. *B*, a small portion of the same, more highly magnified; *tl*, tracheole; *C*, two hypodermal cells from the same; *D*, base and apex of the fifth antecubital trachea, as seen in horizontal section, of another wing of the same specimen; *Sc*, epithelium and intima of one side of subcostal trachea; *a*, *b*, *c*, cells at origin of tracheoles; *tl*, *tl*, tracheoles.

angles of the exterior, and completely occupying the narrower spaces in the wings.

It is also important to note that the basement membrane of the hypodermis of the wing differs in no respect from that of the hypodermis of the body wall, and is continuous with it. In the thinner parts of the wing the two basement membranes meet and fuse, thus forming what has been termed the middle

membrane of the wing. Along certain lines, seen in section in the figure, the two membranes remain separate, and thus are formed the cavities of the wing-veins.

Fig. 84 represents a partial section of a fore wing of a nymph of *Anax junius* two thirds grown; the section was taken at the nodus. The general features here seen are common to the wings of all nymphs—two layers of very elongate, hypodermal cells, which meet in places and form the middle membrane, and remain separate in other places, forming the vein cavities, which usually contain tracheæ. At *B* and *C* in the figure is shown the character of the commoner hypodermal cells.

There is in insects with a complete metamorphosis another type of wing development; this is so different in its external aspects that it may best be described, with respect to these, separately, after which the common fundamental features of wings may be considered.

It has been abundantly shown by others that modification of the type of wing development has kept pace with the increasing complexity of the metamorphosis. The wing-buds are most erratic in the headless, appendageless larvæ of the higher Diptera, Hymenoptera, etc., while they are simplest in larvæ possessing a head, legs, and mouth parts, and especially in those in which the structure is altered least in transforming to imagoes. Among coleopterous larvæ are some in which, save for the appearance of wings, the change is slight; and, indeed, in certain of these (notably the meal worm) specimens are occasionally found with the wings developing externally.

A little coccinellid beetle (*Hippodamia 13-punctata*) has furnished us simpler and more instructive conditions of wing development with complete metamorphosis than have heretofore been fully presented. Fig. 85 shows three early stages in the development of the wings of this insect. Each wing begins as a disk-shaped thickening of the hypodermis (Fig. 85, *A*), which was first observed when the larva was about one fifth grown. A prominent spine, which stands at its dorsal margin, is an excellent landmark to aid in finding it at the first, and when found it is certainly recognized by a slightly concen-

tric arrangement of its cells. It is not at first in connection with nor in approximation to any trachea. The disk elongates and then becomes folded upon itself, thus initiating the wing surfaces. At the time of the folding the wing retreats from the surface, settling down into a pouch-like invagination of the hypodermis (Fig. 85, *C*). Thus it approaches a lateral tracheal trunk, from one of whose smaller branches a few small tracheoles now enter it. As growth continues, the wing extends itself slowly ventrally, as shown in Fig. 86; the mouth of its enveloping pouch becomes somewhat closed by the growth and extension of the pleural hypodermis, but to very various degrees

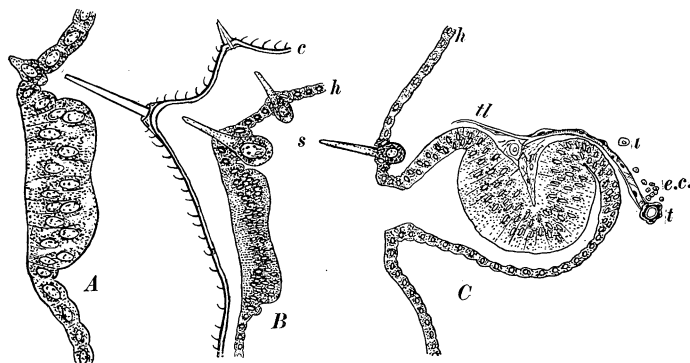


FIG. 85.—Three stages in the early development of wings in *Hippodamia 13-punctata*: *A*, from a larva about one fifth grown; *B* and *C*, from older larvæ, less magnified; *c*, loose cuticle, shown only in *B*; *h*, hypodermis; *s*, spine; *t*, trachea; *tl*, tracheole; *l*, leucocyte; *e.c.*, embryonic cells.

in different specimens, a large part of the larval wing being often found covered exteriorly only by the chitine of the integument.

During the last larval stage the wing is pushed outward and the fold of hypodermis overlying its edges is withdrawn radially, and it emerges from its pouch, becoming greatly extended ventrally under the old larval cuticle, with its walls thrown into numerous folds. When the last larval skin is shed, a still greater expansion transforms it into a wing of the pupa.

Previous to their emergence from the larval wing pockets, there is no appreciable difference between the fore and the hind wings; after this, however, the elytron shows a distinctly

thicker layer of hypodermis on its dorsal side, and the thinness of the hind wings steadily increases with their expansion in area. The hind wings are greatly expanded at the final transformation, while the elytra are almost as large in the pupa as in the imago.

Comparing now the two types of wing development (external and internal), we see that, despite great superficial differences, there are important common features. In both cases the wings arise in early life and form a double plate-like fold of hypodermis, between whose layers tracheæ shortly penetrate. In the former the extension of the wings is gradual and moderate, excepting at the time of transformation; in the latter they early settle down into deep hypodermal pockets, in which their extension is of necessity retarded, although cell multiplication seems not to be.

The principal structural elements which enter into the making of the insect wing are hypodermis, tracheæ, nerves (which, though always mentioned and once or twice figured by other students, we have rarely seen in wings), leucocytes, embryonic cells, and, possibly, sometimes fat cells. Of these, the first two only are essential structures; and these are so important as to merit special treatment.

## II. THE ORIGIN OF THE TRACHEATION OF THE WING.

In wings developing externally like those of a dragon-fly one sees the principal tracheæ passing very early out into the wing-bud, branching freely and forming by multitudinous terminal anastomoses a network of capillary tracheoles. In a horizontal section of a nymphal wing one may see how the branches of the tracheæ are formed. Fig. 84, *D*, is from such a section. It will be observed that the terminal tracheoles are intracellular, the tracheæ intercellular; but that there is easy transition from one condition to the other.<sup>1</sup>

In a wing so mounted that the tracheal system is filled with

<sup>1</sup> There are no such distinct transition cells between tracheæ and tracheoles as Holmgren found (*Anat. Anz.*, vol. xi, pp. 340-346) in the spinning glands of caterpillars, although the cells at *a*, *b*, *c* might seem to stand in the same relation.

air it is easy to see everywhere anastomoses between the distal ends of the tracheoles. This is not shown in our figure; indeed, it is difficult to see it in sections anywhere. The walls of the tracheoles are of extreme tenuity; the best of chitine stains leave them untouched; they are probably protoplasmic tubes at their extremities, such as would best subserve the respiratory process. Tracheoles of this type are everywhere relatively short.

In the much discussed tracheation of the lepidopterous larval wing there are the two well-known systems: the temporary

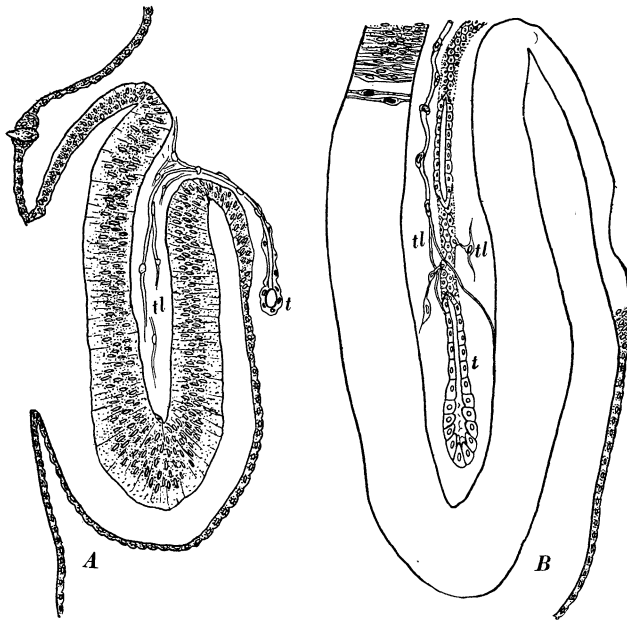


FIG. 86. — Wings of *Hippodamia 13-punctata*, two stages later than those shown in Fig. 85: *t*, *t*, tracheæ; *tl*, *tl*, tracheoles.

system of tracheoles, which enter the wing in the penultimate larval stage and which are functional in the last larval stage; and the permanent wing tracheæ, which grow out into the wings in the last larval stage, but do not become functional until pupation, when they have acquired terminal and lateral tracheoles of their own. In each case the developing air-vessels arise from the epithelium of the lateral tracheal trunk; but they do not communicate with the lumen of this trachea

till after a molt, their mouths being closed at first by the pre-existing intima of this trachea. Fig. 86, *B*, will show clearly that in beetles we have the same conditions, though here the temporary system is much less highly developed. This is from a well-grown larva; *tl* is a tracheole; only such are present in the younger wing shown at *A* in this figure; *t* is a developing trachea; and *tl*, *tl* are developing tracheoles attached to single cells of the wall of the trachea.

We believe that this peculiar temporary system of tracheoles is due to and dependent upon the retention of the wing within the narrow limits of its hypodermal pouch; for its small size alone renders its aëration by simple tracheoles possible. We believe that this also explains the retarded development of the tracheæ. In an externally developing wing it is necessary that the tracheæ should grow with the wing, in order to carry the tracheoles out within reach of the tissues; but when a wing develops internally its length for a long time does not exceed the length of normal tracheoles. In such a wing the tracheæ develop only when needed — at the approach of the time when rapid extension is to take place.

### III. THE BEHAVIOR OF THE HYPODERMIS.

The cells of the hypodermis are remarkable, not only for their secretory and excretory activity, but also for their capacity for rapid shifting and readjustment. Their life history is one of alternating conditions: first, growth beneath a limiting layer of chitine; then, sudden lateral extension when the chitine is thrown off at molting.

The typical hypodermis of prismatic hexagonal cells is found only where the body wall is smooth; in short curves and angles, and in folds of the integument, and in the wings where close crowding is followed by enormous expansion their change of form is very great. At their ends, however, these cells maintain fairly constant relations. Externally they must needs cover the surface to provide its integument, internally they join the basement membrane; between these two planes, however, they may assume almost any shape, according to the conditions of

their growth. Their commoner forms are shown in the figures presented herewith.

The basement membrane consists, we believe, of the fused inner ends of the hypodermal cells or of processes from them. It is often incomplete or fenestrated, and it is of extreme tenuity. Semper thought it (in the Lepidoptera) composed of leucocytes applied to the free inner ends of the hypodermal

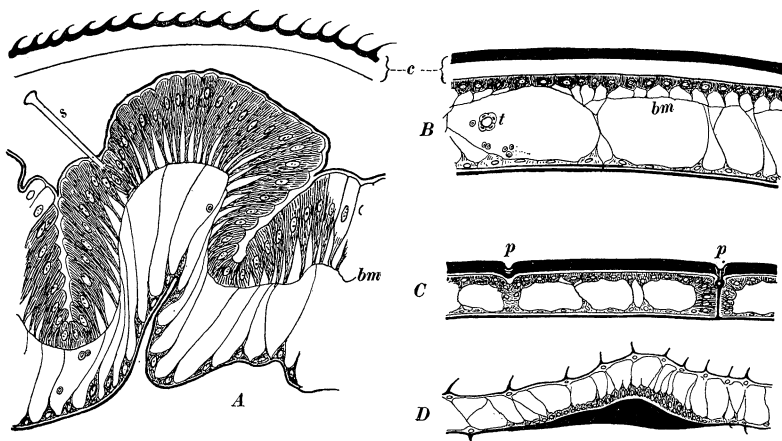


FIG. 87. — Sections of wings of *Hippodamia 13-punctata*, all drawn to the same scale: *A*, from full-grown quiescent larva, a bit of the wing crumpled under the loose larval cuticle; *s*, a deciduous spinule; *bm*, basement membrane; *B*, fore wing (elytron) of an old pupa; *C*, fore wing of a newly transformed imago; *p*, pits above the chitinous pillars; *D*, hind wing of a newly transformed imago, showing especially the manner of formation of a special chitinous brace.

cells, and his opinion has been concurred in by several subsequent investigators; but we are inclined to believe that in the forms we have studied, the formation of it from leucocytes is at least exceptional, for the following considerations:—

1. While leucocytes are not infrequently seen lying against it, we have seen no direct evidence of their participation in its development.

2. During early stages it is well formed and *destitute of nuclei*.

3. In later stages, when, after the expansion of the wing, it contains distinct nuclei, there is evidence that some of these at least are derived from the hypoderm cells whose nuclei, once crowded up to this level, have remained stranded there after the expansion of the wing.



In past accounts of hypodermal development in wings too little attention has been paid to the mechanics of the developmental process—to the varied conditions under which the cells labor in successive stages. To these conditions are mainly due the different cell forms seen; and, except where like conditions are compared, different series will be contradictory. A study of hypodermal ontogeny in the wings of representatives of half a dozen orders of insects convinces us that it is impossible to summarize the process except in the most general terms.

In very early stages in externally developing wings there is found a condition of the hypodermis not far removed from the normal. The cells are only a little less prismatic, a little more columnar or rhomboidal, and the two layers meet internally in very limited tracts. Fig. 89, *A*, is from the wing of a young acridid nymph. It would answer almost equally well for a

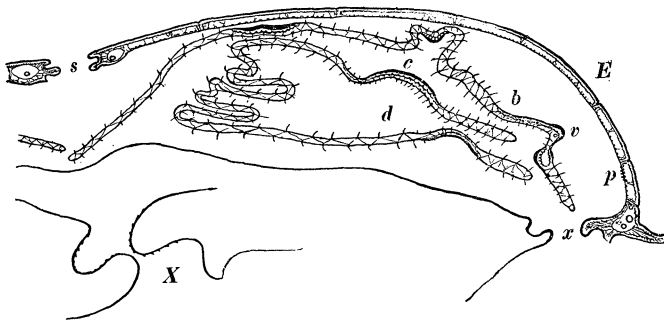


FIG. 88. — Cross-section of wings of a newly transformed imago of *Hippodamia 13-punctata*, *in situ*: *E*, fore wing; *b*, basal portion of hind wing; *d*, distal, reflexed portion of hind wing; *s*, elytral suture; *v*, a vein; *c*, a cuticular thickening; *p*, stridulating (?) processes; *x*, the interlocking ridges, seen more magnified at *X*.

young nymph of the dragon-fly, *Gomphus*, or for several ephemerids we have studied; or, for that matter, for parts of the ephemerid tracheal gill or for its operculum; or, save for the lack of tracheæ, for the overlapping edge of the prothorax or for a section of the labium.

This early condition is followed by a long period of growth, during which the hypodermal cells become crowded and much more elongated, their nuclei, which were originally nearer their inner ends, coming to occupy a spindle-shaped middle portion in the cells (Fig. 84). The crowding is excessive, and the effect

of it in massing the cells much more marked, of course, when wings are developed internally. But even here the spindle-form cell is recognizable (Fig. 86, *B*), and all the cells appear still to extend from surface to surface of the hypodermis.

The first great expansion of the wing occurs just before pupation, with insects having complete metamorphosis, but not until the final transformation, with those in which the metamorphosis is incomplete. This expansion results in the broadening of the bases of the hypodermal cells, in the settling down of their nuclei close upon the chitine layer, and in the drawing out of their inner ends into a long, slender prolongation, which

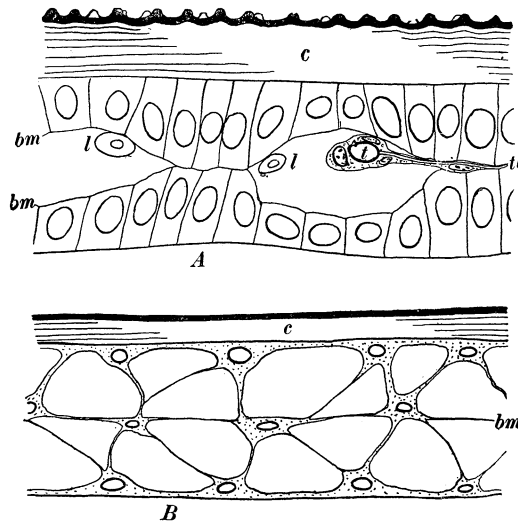


FIG. 89. — *A*, cross-section of the wing of a young acridid nymph: *c*, cuticle; *bm*, *bm*, basement membrane; *t*, trachea; *tl*, tracheole; *l*, leucocyte; *B*, stellate cells in hypodermis, from the anal angle of a wing shown in Fig. 83.

generally retains its attachment to the basement membrane, and thus to its neighbors opposite, in those portions of the wings where the membranes are united. The cells thus become peaked in appearance. Their breadth and height will depend, however, on (1) the extent of the previous crowding; (2) the extent of the surface they are now called upon to cover; and (3) the width of the space they are now called upon to bridge. When, through excessive crowding, some of the innermost

nuclei have come into contact with the basement membrane at the subsequent expansion of the wing, these, instead of retreating with their fellows to the chitine layer, seem instead to remain where they are, and to attract to themselves the slender prolongations of the neighboring cells. They thus acquire a stellate appearance, as shown in Figs. 89, *B*, and 90, *D*. These seem to occur only in narrow spaces, in which great expansion has followed close crowding.<sup>1</sup> We have found them in *Leucorhinia* (Fig. 83) in the rapidly expanding anal angle of a wing, the greater part of which appeared as Fig. 84, *B*, the cells having spindle-shaped bodies. We have seen them also in the anal angle of the wing of a pupa of *Corydalis*,

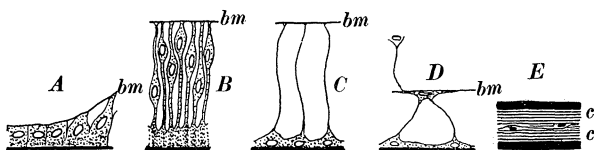


FIG. 90. — Diagram illustrating the behavior of the hypodermis during the development of an insect wing: *A*, nearly normal hypodermis; *B*, the same, after being crowded within the wing fold; *C*, the same after the first great expansion of the wing; *D*, a cell stranded upon the basement membrane; *E*, disappearance of the hypodermal cells with chitine formation.

the pre-anal area being filled with the peaked cells more characteristic of that stage.

The segregation of the hypodermis, which results in the accumulation of it around the tracheal channels and in those parts of the wing to be made strong by heavy deposits of chitine, takes place during the final stages. Some interesting illustrations of it are shown in Figs. 87 and 88, and are explained in the legends to the figures. These processes and the final disappearance of the scattered hypodermal cells, wasting themselves away in chitine formation, are the final steps in the making of the wing.

The accompanying diagram (Fig. 90) will, therefore, represent what we think may fairly be taken as typical for the behavior of the hypodermis. While this strongly suggests

<sup>1</sup> This is the "Grundmembrane" of Semper, which was believed by him to be formed by leucocytes during the pupal period, and, therefore, to be distinct from the middle membrane of the wing of the larva.

ontogeny, we desire explicitly to state that we believe these changes to accompany certain conditions under which cells are placed, rather than any particular stages.

#### IV. THE TRACHEÆ AND THE HYPODERMIS.

After discussing these two separately, there remain a few interesting features of their correlated behavior to be noticed.

In all insect wings the two plates of hypodermis constituting the wing fold are at first separate, *i.e.*, not fused internally. At the time when the tracheæ enter the fold the two layers become approximated along lines midway between the tracheæ, resulting in actual fusion of the internal ends of the cells. We have already shown in *Psocus*<sup>1</sup> (and have seen in several other insects) the external evidences of the gradual lateral extension of the fused area to delimit definitely the channel through which the tracheæ pass. The term "cuticular thickenings" has been used hitherto to designate the pale bands along the tracheæ, and the veins to be formed here will be, of course, cuticular thickenings; but until the veins are formed (and this does not occur until the final molting) the term is inaccurate and misleading. A glance at Fig. 84, *A*, will discover that the hypodermis is in the earlier stages actually thinner here than elsewhere. It is only at transformation to the imago that the cells become aggregated about these channels and form there the dense chitine of the veins. The pale color of the bands, indicating the extent of the vein cavities when viewed by transmitted light, is doubtless due to the fact that the hæmolymph filling these cavities is more translucent than the hypodermal tissue which completely fills the wing elsewhere.

But, returning to the earlier stages, we have seen that, in wings developing externally, the hypodermis encloses the tracheæ in channels which ultimately become veins. It is now to be noted that there are often channels present which do not contain tracheæ. This is oftenest true of two large channels at the lateral margins of the wing (Fig. 84, *A*). Of these the costal remains abundantly lined with cells, which

<sup>1</sup> *American Naturalist*, vol. xxxii, p. 241, Figs. 11, 12.

ultimately form the strong costal vein. Its trachea is often atrophied, probably owing to the disadvantageous position of its base in relation to air supply, as we have hitherto indicated. The anal channel becomes obliterated, and the dense hypodermis of its walls dispersed by subsequent expansion of this part of the wing. In some wings in which this space persists, as in *Psocus*, it is occupied by the third anal trachea.

In wings developing within small hypodermal pockets, while the cells are densely crowded and while the fusion of the cells internally joining the two layers is more tardy and incomplete, the same principal channels are formed. In the *Lepidoptera*, though the development of their tracheæ is retarded, the temporary tracheoles pass out in tangled skeins through the original channels.

But the process of reduction of tracheæ, already begun in the lower orders, finds favorable conditions for progress in the shorter and more open wing sacs developed internally; and we find in all but the more generalized members of certain orders that the close correspondence between tracheæ and channels due to simultaneous development is again lost. Illustrations have been abundantly offered in preceding chapters; we are here offering only a suggestion as to the reason, first for this correspondence, and then for the loss of it. While the tracheæ seem at first to have been the determining factor in the venation, and while we have been able to show a gratifyingly large number of cases in which the tracheæ show the unmistakable signs of homology, and cases in which the course of the veins is still determined by them, it appears that in certain insects the tendency of the hypodermis to segregate itself and to form chitine along certain lines has become so well established as to be more or less completely independent of the tracheæ. The veins have to do in these cases with locomotion in adult life; the tracheæ, with growth and metamorphosis. The adult wing, whatever it may have been originally, has become a dry resilient plate of chitine traversed by finely adjusted supports. It would be manifestly disadvantageous for the tracheæ to follow the course of these supports, sharp angled, and often recurrent; but in wings with slight fusion between

the walls this is unnecessary. The disappearance of distinct tracheal channels has restored open competition between the tracheæ, which accounts for the more rapid disappearance of all save those most favorably situated in relation to the source of the air supply — usually only two in the most specialized insects, which still stand as representatives of the two groups of tracheæ with which we begin our series.

Fortunately for the study of homologies in insect wings, the veins had attained an arrangement so useful that it could be held by natural selection after the tracheæ had ceased to determine their position.